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FLORAL EVOLUTION IN THE RANUNCULACEAE

E.E. LEPPIK

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FOREWORD

One of the most puzzling chapters for the botany student through the years has been the origin and evolution of colored blossoms of flowering plants. The sharply contrasting colors and intricate forms are peculiar to green plants, whose "fundamental task" in nature is photosynthesis and whose characteristic color is due to the green pigment, chlorophyll. One can observe that showy blossoms function as attractions for pollinating insects, but until very recently no one had proposed a satisfactory working hypothesis for the development of flowers to their present forms and colors.

In 1941, R.J. Pool in his textbook, "Flowers and Flowering Plants," characterized the situation as follows:

"The esthetic appeal of flowers to the human certainly depends on their harmonious combinations of colors, their peculiar symmetry, delicate constructions, and pleasing odors. But we cannot expect a similar conception of beauty, based on a high order of intelligence, among pollinating insects. We know that insects do not "enjoy" flowers for their color or odor, but for the food that they secure. Further investigations may remove some of the "romance" from this alluring field, but they will probably endow it with even a greater wealth of definitely established scientific truth than is at present available."

To unlock this botanical strong box, a scientist was required with unusually broad interest, a wide range of biological experience, a command of several languages, uncommon powers of observation and a determination to publish his conclusions. In Dr. E.E. Leppik are combined these traits and more. After many years of effort to bring order to the gray zones between several scientific disciplines and in spite of interruptions from war and threats to personal safety which forced him and his family over several years to move from one country to another, he continued his observations.

His exploration into the mysteries of flowers has been both an exciting adventure and a successful scientific accomplishment. During numerous travels in Europe, Africa and North and South America he gathered data on flower types and their pollinators from all geographic zones, arctic to tropic. This material enabled him to propose a new system for classifying flower types and to relate it to the development of insect groups that act as pollinators. The system revealed a sequence of floral evolution from the simple, elementary types to the complicated floral structures of the higher angiosperms which paralleled the sensory development of the pollinating insects. Implied is a reciprocal correlation between the evolution of flower types and the sensory development of their pollinators.

As support for his hypothesis, Dr. Leppik presents evidence gathered from fossilized flowers and floral imprints in amber, compact clays, silts, muds, and very fine sands. In several papers (1960, 1961b, 1963a, b) he discusses the fossil evidence for floral evolution available at present.

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Particularly significant is the reconstruction of a Cretaceous mag-
nolia-like flower collected from the Dakota sandstone. This is the oldest
known floral structure of an angiosperm which shows the size, form and
symmetry of a haplomorphic flower of the Cretaceous period. This was
reported in Advancing Frontiers of Plant Sciences (Leppik, 1963a).

Under a research project entitled, "The Evolutionary Relationships
Between Plants and their Environment," in the Department of Botany
and Plant Pathology of the Iowa Agricultural Experiment Station, Dr.
Leppik has published a series of papers that brings light on the old
mystery of floral evolution. Interest in his work is being expressed by
scientists in several states and foreign countries. All provide encour-
agement for him to continue his efforts.

- W. H. Bragonier

# FLORAL EVOLUTION IN THE RANUNCULACEAE[1]

E. E. Leppik

Iowa State University, Plant Introduction Station, Ames, Iowa

ABSTRACT. Six clearly separable evolutionary levels in the floral evolution of the Ranunculaceae were found to coincide with the six corresponding stages of sensory development of their pollinators as follows: amorphic →haplomorphic→actinomorphic→pleomorphic→ stereo - morphic→zygomorphic. This is a basic trend of floral evolution, fully recapitulated in a single family. Except for the first (amorphic), all upper levels are represented in the present-day floras as clearly separable type-classes. They are therefore accessible to direct observations and experimental study. Extensive statistical data on flower visitors of the Ranunculaceae confirm the proposed theory of the mutual interrelationship between the evolutionary levels of flower types and sensory stages of pollinating insects. The new picture, obtained by this study, gives us a better understanding of the evolutionary relationship between insects and plants and explains the extreme diversity in the floral structure of the Ranunculaceae.
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## INTRODUCTION

Most taxonomists (Bessey, 1897, 1915; Hallier, 1905; Glück, 1919; Hutchinson, 1923, 1926; Tippo, 1942; Cronquist, 1951; Eichler, 1958; Eames, 1961a, b; Thorne, 1963) today consider the family Ranunculaceae to be a natural taxon with well-preserved primitive characteristics of a phylogenetically lowermost group among herbaceous dicots. Still more elementary, in this alliance are several woody families and the aquatic Nymphaeaceae. In the conventional phylogenetic systems the order Ranales, accordingly, is placed at the bottom, and most remaining groups of higher angiosperms are derived directly or indirectly from the ranalian roots.

From the related families, such as Lardizabalaceae, Magnoliaceae, Winteraceae, and Degeneraceae, the Ranunculaceae are distinguished

mainly by their herbaceous habit and more advanced floral structure.
But, even in these points, the lowermost members of the herbaceous
line, like the section Moutan of the genus Paeonia, are scarcely separ-
able from their woody relatives. These Chinese tree-peonies are char-
acterized by shrubby habit, magnoliaceous wood anatomy, and large
magnolioid flowers, thus representing an intermediate link between
woody and herbaceous members of the order Ranales. Hence it appears
that the Ranunculaceae as a whole are a distinct phylogenetic group,
having a considerable number of primitive characteristics in a single
family.

   Contrary to this stable phylogenetic position, an extreme variability
exists in the floral structure and in the typological differentiation of
flower types in the Ranunculaceae. In this moderately large family of
35 genera and about 1500 species, five type-classes are represented in
a successive sequence, beginning with elementary haplomorphic and
ending with highly specialized zygomorphic flower types (see Figs. 1, 3).
Such typological diversity is not known in any other euanthial family of
dicots, but occurs in the monocot order Liliiflorae. Among pseudanthial
plants, however, similar evolutionary sequence is fully recapitulated
in the graded series of the flower heads of the Compositae and partly
repeated in the cyathia of the Euphorbiaceae, in the inflorescences of
the Umbelliflorae, and in other families with compound flowers.

   Thus, the phylogenetic stability of main morphological characteristics
of the Ranunculaceae is compensated with an ever-changing hologenetic
course in the floral evolution. Hence, the hologenetic[2] approach to the
problem, as attempted in this study, could help toward final understand-
ing of floral evolution in the Ranunculaceae. Such an attempt, conse-
quently, is of interest in itself and has importance because of the key
position assigned to the Ranunculaceae in the classification of angio-
sperms.

   However, the main reason for a re-examination of floral differentia-
tion in the Ranunculaceae is the new prospect of correlating floral evo-
lution with the sensory development of pollinating insects, as described
elsewhere (Leppik, 1957b, 1960b, 1961b). Recent investigations show that
insects and flowers are closely and mutually interrelated in evolution as
reciprocal selective factors, adapted to each other and to their particu-
lar environment. Ample evidence is now at hand that color and shapes
of flowers have been evolved in response to, and in association with, the
sensory evolution of insects as flower feeders (Baerinds, 1950; Leppik,
1957b; Thorpe, 1956, p.204). It is highly desirable, therefore, to ar-
range the directly observable tendencies and obvious trends of floral
evolution in the Ranunculaceae into a typological[3] sequence, which would
represent the general evolutionary trend of the angiosperm flower, and
would mirror the sensory development of contemporary pollinators.

   The much debated question, whether all angiospermous plants, in-
cluding Pandanales, Principes (Palmae), Amentiflorae (Salicales), Casu-
arinales, and Piperales are of monophyletic or polyphyletic origin, is

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[2] Hologeny is the genesis and historical development of the biotic whole
   or holon (Leppik, 1948a, 1957c).

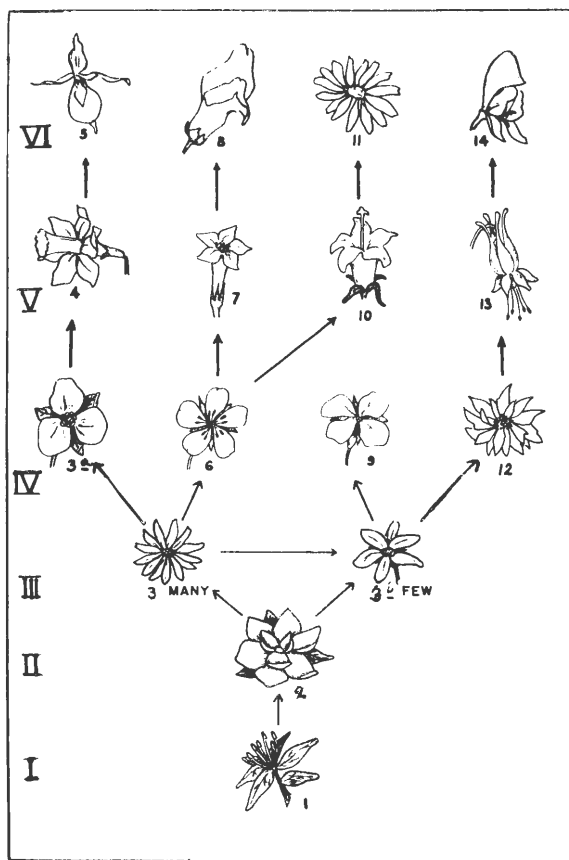[3] Typology is the science that deals with plant (flower) types.

Figure 1. Historic sequence of floral evolution. I level: amorphic flower types; II level: haplomorphic; III level: actinomorphic; IV level: pleomorphic; V level: stereomorphic; VI level: zygomorphic (according to Leppik 1957b, p.472).

recently discussed again by Hughes and Couper (1958), Li (1959), Hughes (1961), and Meeuse (1962, 1963). Meeuse, for instance, suggests a poly-phyletic descent of present-day angiospermous plants from ptotocyca-dopsid and bennettilalean affinities. According to this author angio-sperms "might have developed through adaptive evolution caused by the changeover from anemophily to entomophily, i.e., by the advent of the intimate reciprocal association of flower types with protected ovules and the corresponding pollinating insects." Many parallel developments (convergencies) in floral evolution would support this view. Selective activity of pollinating insects tends to form similar floral structures in unrelated plant groups such as Bennettitales and Angiospermae (Leppik, 1960b) or in distantly related angiosperms, such as Magnolia, Nymphaea, Nelumbo, etc. In other cases for the same reason different flower types may evolve in the same genera, as in the present-day Magnolia (Leppik, 1963a). In general, pollinating insects are searching for their food plants not according to phylogenetic characteristics, but select for their visits, flowers of certain colors, size, and symmetry. These are typological characteristics that may or may not appear on phylogenetically related plants. As a result, similar flower types develop in phylogenetically unrelated plant groups (convergency), as would be expected in the case of polyphyletic origin of angiosperms.

The fact of a mutual adaptation of flowers and pollinators to each other was well known to classic students of floral ecology, such as Koelreuter (1761), Sprengel (1793, 1811), Darwin (1862), Delpino (1869, 1875), Müller (1883), Loew (1884), and Knuth (1908). Modern floroecologists and in-sect behaviorists, including Frisch (1914-1954), Baerinds (1950), Thorpe (1956), Jaeger (1957), Pijl (1960-1961), Percival (1962) and others almost unanimously stress the profound significance of the selective activity of pollinators to the evolution of flower types. But almost all recent writers hold the view that the evolution of flowering plants is still as great a mystery as ever. At least such viewpoints are expressed by Just (1939, 1952), Pool (1941), Good (1956), and again by Pijl (1960, p.414).

In fact much of this "mystery" is removed now, partly by an exact experimental study of the sensory behavior of insects, partly by the better understanding of the evolutionary relationship between insects and flowers. The proposed new theory about the existence of a conjectural sensory mechanism in insects that governs their tropheclectic behavior and selective activity is substantially supported by reliable observations and experimental study. Recent investigations (Leppik, 1957b) suggest that this conjectural mechanism (or mechanisms) has been established in insects step by step during their sensory evolution, and is functioning now as the principal determining factor for floral differentiation. A sub-sequently elaborated historical sequence of floral evolution is adequately evidenced now by paleontological records. Eventually a new system for classification of flower types is available now for field work and for testing the ability grades of pollinating insects and other visitors of flowers. Main results of this extensive study are discussed in several previous reports which are cited at the end of this paper (Leppik, 1948-1963). These reports also served as basis and background for the pres-ent exploration on the floral evolution in the Ranunculaceae.

## HISTORICAL REVIEW

This paper is one in a series of reports published by the writer about an experimental study of the evolutionary relationship between anthophilous insects and entomophilous plants (Leppik, 1948-1963). Unfortunately these reports are not assembled in any easily accessible review journal, but are scattered throughout diverse periodicals in this country and abroad. Some older issues are long out of print.

These circumstances may justify some repetitions and occasional restatements of earlier findings in this paper that could help the reader better to comprehend the subject as a whole. For the same reason it appears desirable to add a brief historical review of earlier experiments and field observations that expanded considerably our knowledge of the sensory behavior of pollinating insects and helped to build up our present concept of floral evolution (see "Introduction").

### Some Newly Observed Sensory Capabilities of Insects

Until recently, little was known about the sensory abilities and mental faculties of pollinating insects. Joseph Gottlieb Koelreuter (1761), Christian Konrad Sprengel (1793-1811), the brothers Hermann and Fritz Müller (1866-1896), Charles Darwin (1862), Frederico Delpino (1869-1875), Ernst Loew (1884), and other early floroecologists proved that insects are attracted by the variegated colors and fragrant odors of flowers but they did not know exactly how and why. Neither could they explain the enigmatic development of flowers to the present level of perfection, nor could they comprehend the esthetic appeal of colored blossoms to the nectar-seeking insects.

More recent experiments and observations by Grant (1949-1952), Kugler (1952-1955), Ribbands (1953), Pijl (1961), Butler (1954-1959) and others proved an unchangeable constancy of certain groups and a relative steadfastness of many individual pollinators to definite flower types. In a bee colony all workers ordinarily gather nectar or pollen from the same flower type, and every hive has a "harvest formula" of its own. Subsequent to these findings a new problem arose: how can bees distinguish and memorize complicated floral structures, displayed to them in hundreds of combinations in a foraging area?

Present extensive experimentation in the field of sensory physiology of insects has brought a considerable change into this unclear situation. Since the rediscovery and scientific explanation of the "dances" of honeybees by Karl von Frisch (1914, 1950, 1954) several new phenomena and remarkable facts have been learned about the complicated life and behavior of pollinating insects.

An efficient system of communication, a "sign or dance language" of the bees (Ribbands, 1953; Lindauer, 1961) and some emotional reactions, are discussed in some earlier papers (Leppik, 1953-1955). Several new senses, instincts and a surprisingly high level of sensory capabilities of pollinating insects belong to the further noteworthy discoveries made during the last decades.

Not less astounding are the recently recorded abilities of bees and other insects to find their way by means of the polarized light, and to

detect the ultraviolet rays from the white light (Ribbands, 1953). These outstanding properties of the compound eye of arthropods lie, of course, far beyond the range of ability of the simple eye of man and higher animals. In other respects the mammalian eye is believed to be superior to the compound eye of insects.

A further series of experiments and observations of the writer led to the deciphering of a well-established and widely distributed system of recognition of numeral patterns ("iconic numerals") and definite symmetrical structures ("semaphylls") of insects. Although this system existed in nature for many millions of years, its origin and purpose was until recently unknown to man. There are thirteen basic symbols in this system, which vary further in their size, color and symmetry. Several hundreds of definite combinations are in this way clearly distinguishable to the insect eye (Leppik, 1948a, 1953b, 1955b).

Using the above-mentioned system of iconic numerals as a standard, a method is available now to determine the relative sensory capabilities of different groups of pollinators and to establish the stage of their sensory development, as described elsewhere (Leppik, 1956a, 1958).

## Experiments with Bees and Nerve Poisons

Dr. Gerhard Schrader (1951a, b) of Leverkusen, Germany, is the successful discoverer of several new chemical compounds that act on man, animals, and insects as the most fatal nerve poisons ever known. One of his new chemicals, diethyl-p-nitrophenyl monothiophosphate, appeared capable of producing a strong sensory reaction in insects, and therefore is briefly discussed in this paper. This is an ester of thiophosphoric acid with the empirical formula $C_{10}H_{14}NO_5PS$. Commonly the structural formula is used, as follows:

$$
\begin{array}{c}
C_2H_5O \\
\phantom{C_2H_5O} \diagdown \\
\phantom{C_2H_5O} \diagup \quad P \cdots\cdots O \cdots\cdots \langle \ \rangle \cdots\cdots NO_2 \\
C_2H_5O
\end{array}
$$

This new substance which was discovered in 1944 is widely used now as a powerful insecticide of almost universal application range. In Europe it is sold as "E 605," which is the former secret code number of this substance in Germany. American "Parathion" is a methyl ester of the German E605. "Thiophos" is the trademark for technical parathion manufactured by American Cyanamid Company as wettable powders and dilute dusts. They are sold under different brand names by various dealers throughout the country. Lately both products, diethyl and dimethyl parathion, appeared on the American market.

Both dimethyl (E 605) and dimethyl (thiophos) parathions owe their lethal activity to their ability to inactivate the cholinesterase, an enzymatic substance in nerve cells. Soluble in lipoids, parathion can pass through nerve axons and accumulate in nervous systems. The theory of the inhibitory process has been developed by Wilson and Meislich (1955) in accordance with the process of enzymatic hydrolysis.

Nerve Poisons are Disastrous to Bees
and Other Pollinating Insects

The loss in bees rose correspondingly with the increased application of E605 dust in Germany.   In 1949 the Agricultural Department in West Germany registered a total loss of 20,000 bee colonies in one season. In addition other beneficial insects that act as plant pollinators were killed by mass application of new nerve poisons.   Yet the beneficial effect of nerve poisons as powerful insecticides was so decisive that their application increased rapidly, in spite of many accidents and claims from beekeepers.  After the war, they were promptly introduced to America and are used now throughout the world.

"The Struggle of Bees" (see Plate 21)

A series of laboratory experiments with E605 revealed some hitherto unknown sensory reactions in honeybees. Tiny amounts of these poisons were able to release strong emotional reactions as were demonstrated in a strange phenomenon, called "the struggle of bees."  This is a general alarm and turmoil among bees, accompanied by fierce battles in which thousands of partakers are killed.   The "struggle" of honeybees was first observed in Bavaria and was demonstrated in an experimental apiary of the State Horticultural College in Weihenstephan by the writer and his co-workers in the year 1948 (Leppik, 1949-1954; Palm, 1949).
Later on "the struggle of bees" was frequently observed as a result of misuse of E605 dust as insecticide.  Bees collected poisonous dust from treated plants and carried it to hives, thus starting a "struggle" in their home colonies.   Ten marked worker bees that were loaded with E605 dust started the "struggle" in an experimental hive during which most inhabitants of a hive of 40,000 were killed during an afternoon. The struggle of bees caused great losses in honeybees in Germany, until better methods of application and some restrictions in the use of nerve poisons were introduced.   In America mostly wettable powder of dimethyl parathion is used and is less hazardous to bees than the E605 in powder form as used in Germany.   Nevertheless several mass killings are reported from the United States by Knowlton (1951) and Leppik (1951d), and the "struggle of bees" by Leppik (1951d, 1953a, 1954b).
"The struggle of bees," as a remarkable phenomenon in the social behavior of bees, gave rise to vivid comments in newspapers and scientific journals in all parts of the world. This writer has seen many press reports from Europe, North and South America, India, and Australia. More scientific comments about this discovery were made by Merkenschlager (1950, 1958), Bolle (1952, 1954), Kaempffert (1953, 1954, 1955, 1956), Mehlisch (1954) and anonymous writers in Scientific American (1951, 185(2):34-36), and in The Organic Farmer (1953, 5(1):44-46).   In Germany the "struggle of bees" as a phenomenon was confirmed by von Frisch and demonstrated experimentally by his coworker Schick (1953).

Foraging Behavior of Honeybees

Until now the flights of individual bees have been observed in certain

flowering plants that offer nectar or pollen to their visitors.   Much val-
uable information about the flower visitors of numerous plant species
has been gathered in this way and published in voluminous monographs
and manuals by Delpino (1869), Müller (1883), Knuth (1908), Robertson
(1928) and others.   Von Frisch (1914-1954) with his students and co-
workers introduced the method of marking of individual bees with colored
spots for field observations.   The efficient system of communication of
honeybees has been deciphered in this way.   However, all these methods
have a restricted area of application for observation of the activity of
individual bees only.   Experimentation with nerve poisons opened a new
way to  study population behavior in large masses of pollinating insects.
Application of nerve poisons in certain areas revealed common behavior
traits of insect population in this area, as illustrated in the following
example.   (See Plate 20.)

### A Disaster with Nerve Poisons

    In Bavaria, a dusting of a small field of about an acre of blooming
rapeseed (Brassica napus L. var. oleifera DC.) with potential insecticide
caused a mass killing of honeybees within a radius of 2-3 miles  around
the dusted field.  About 5 million bees belonging to several beekeepers
were killed during a short afternoon.   Closer analysis of affected bee-
hives showed that most worker bees, sometimes as many as 10, 000 in a
colony, were killed. But in some nearby hives not a single bee was hurt.
    The distribution of beehives around the dusted rapeseed field (black
square) is sketched in Figure 2.  Beehives with total loss of worker bees
are shown in black, those where no dead bees were found during and
after the dusting of the field are  shown in white.   Arrows indicate the
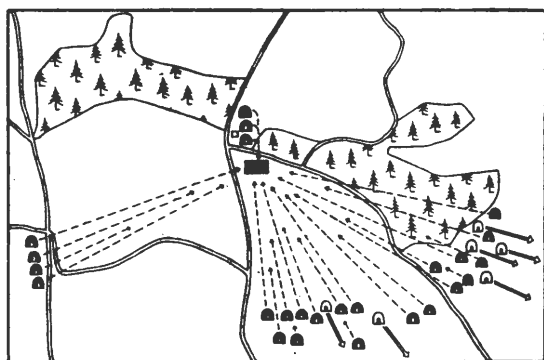flight direction of worker bees during their foraging trips.



Figure 2.   Map showing the distribution of beehives around the rape-
            seed field (black square) dusted with deadly poison.   The hives
            with total loss of worker bees are colored black.   White hives
            indicate that no dead bees were found during and after the dusting.
            Arrows point flight direction of worker bees during their foraging
            trips.

From this sketch it appears that in many colonies that were oriented to the poisoned rape field, all or most workers were killed shortly after dusting. Some few colonies, however, that were oriented to other plants, survived and did not show any losses at all. This indicated the great regularity and strict order in a bee colony during their foraging activities.

From this and further experiments it appeared clearly that in a bee colony all worker bees, sometimes as many as 20,000, were oriented to the same place (rape field) and collected nectar from the same plant species (rape), not touching other flowers during their successive trips. To find their proper foraging area, these bees had to fly as far as 2 to 3 miles and to locate their food plants in a small area between forests and fields.

Later, similar experiments were performed with marked bees that enabled the registration of workers from different colonies on the same foraging area. From these experiments it appeared that every bee colony had its definite food plant in a restricted foraging area, which was exploited as long as the nectar flow in these plants were still satisfactory. Other colonies worked in the same way but with other plants. How such perfect organization is possible was demonstrated by von Frisch to be a precise system of communication among bees.

Thus the extensive experimentation with nerve poisons, although accompanied by serious disasters, helped to demonstrate the actual relationship between flowers and their pollinators. This understanding and further investigations with tropical insects in El Salvador (1953, 1954) led the present writer finally to a new concept of reciprocal correlation between the evolution of flower types and the sensory development of pollinating insects, as discussed in the following chapters. (See Plate 22.)

## DEFINITIONS AND TERMINOLOGY (Figs. 3-6)

Since the term "flower" (euanthus[4]) has been used in botanical literature with various and sometimes controversial meanings, some brief terminological remarks here appear desirable. Additional comments on the classical theories and modern concepts of the nature of the flower can be found in papers published by Bancroft (1935), Arber (1937), Wilson (1937), Gregoire (1938), Plantefol (1948), Parkin (1951), Tepfer (1953), Good (1956), Mason (1957), Barnard (1960, 1961), Eames (1961a, b), and Melville (1960, 1963).

The word "flower" (Latin: flos, Greek: ἄνθος German: die Blume, etc.) very likely had already been used in prehistoric times in various languages to indicate the showy blossom or a plant grown or esteemed for its showy blossoms, i.e. an ornamental. This is still the common meaning and the valid definition of a "flower" in a gardener's vocabulary.

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[4] Euanthous plants bear true flowers composed of semaphylls and sporophylls. Pseudanthous plants carry pseudo-flowers, inflorescences that imitate true flowers, such as the flower head of the Compositae, cyathium of the Euphorbiaceae, involucre of Dichromena, and so on (see Figs. 3-6).

Any purpose of showy flowers other than to express beauty very likely was inconceivable to ancient peoples.

Although the "caprification" (transferring of pollen from "caprificus" to "ficus") of fig trees by a chalcid wasp for better setting of fruits was already known to Aristotle (384-322 B.C.), the true meaning of insect pollination was not understood before the sensational discoveries of Koelreuter (1761) and Sprengel (1793) in the middle of the eighteenth century. The phenomenon of "caprification" was later described in detail by Laubach (1882) and the wasp involved was identified as Blastophaga grossorum Grav. (= Cynips psenes L., Chalcididae). Some ceremonial pollinations, performed by ancient Egyptian priests, were obviously inaugurated by religious conviction, rather than by an understanding of the process of fertilization.

After a comparative morphological study it became apparent that the essential parts in flowers are the reproductive organs, stamens and pistils (i.e. sporophylls), and that the showy envelopes are present only in complete flowers for attraction of pollinators. Thus, the term "flower" lost its original meaning and in scientific literature became synonymous with the reproductive structure of seed plants (Anthophyta).

A flower then was considered to be a reproductive shoot composed of sporophylls and perianth. Supporters of the strobiloid theory went still further, defining a flower as a specialized "anthostrobilus,"[5] in which the lower sporophylls have become sterile, forming sepals and petals, and the upper have changed into stamens and carpels. Consequently, the main interest was centered around the morphological structure of reproductive parts rather than the ecological aspects and physiognomy of a flower as a whole. The corolla, for instance, almost lost its position as a morphological entity, because petals were considered sterile stamens, metamorphosed bracts, or petaloid sepals (see Smith, 1926, p.26). All flowers were classified then as complete (with sepals, petals, stamens, and pistals) or incomplete (some regular organs lacking), perfect (with stamens and pistils) or imperfect, petalous or apetalous, sepalous or asepalous, and so on. Various theories that interpret flower as a morphological unit, including a new gonophyll concept, are recently reviewed by Melville (1962-1963).

Such one-sided emphasis on morphological principles did not favor the study of the evolution of flower types, but rather has produced some contradictions in morphological and typological concepts. The actual evolution of flower types to their present-day perfection of color, form, and symmetry remained as great a mystery as ever. And, thus, the deviation from the original aesthetic conception of the word "flower" to a morphological abstraction, in spite of adding clarity, has resulted in several misconceptions and controversies among students of floral ecology.

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[5] Anthostrobilus is according to Arber and Parkin (1907-1909), a hypothetical cone-like flower that precedes gymnosperms and early angiosperms. Flowers of primitive angiosperms, such as Magnolia, waterlily, and many other Ranales can be derived from anthostrobilus. More fundamental in conception is the recent gonophyll theory of Melville (1960).
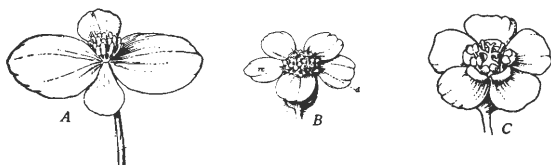
Figure 3. Flower of _Begonia_ (A) compared with the flower head (pseudo-flower) of _Achillea_ _millefolium_ L. (B) and cyathium of _Euphorbia_ _corollata_ Engelm. (C). Note the striking similarity of these "flowers" in spite of being composed of different morphological organs. (Courtesy of Ginn and Company, New York.)

Shown in Fig. 3 is a "true" flower (euanthus) of _Begonia_ (A) in comparison with an inflorescence (capitulum) of _Achillea_ _millefolium_ L. (B) and with a cyathium (inflorescence) of _Euphorbia_ _corollata_ Engelm. (E). In these very similar configurations only _Begonia_ has morphologically true petals that form the showy part of a flower and serve for attraction of pollinators. In the flower head or capitulum of the Compositae petals are replaced by ray florets and in the cyathium of the Euphorbiaceae by colored bracts. Consequently the pseudo-flowers of _Achillea_ and _Euphorbia_ are incomplete and imperfect morphologically, but are entirely perfect and complete typologically. Such "pseudo-flowers" can easily be mistaken for "true" flowers by the layman. This example clearly shows the difference between morphological and typological conceptions.

The striking similarity of the cyathium of _Euphorbia_ _corollata_ Engelm. with the single flower of _Spirea_ _trilobata_ L. is shown in Plate I. Both structures are strictly pentamerous, have white color with yellow center, and have very closely the same size.

Fig. 4 shows the cross section (B) of the flower head (capitulum) of a yarrow (_Achillea_ _millefolium_ L.) and details of the individual florets (C, D). From a distant view this structure imitates a single flower (A), but is actually composed of many disk florets and rays (rc). Although disk florets have preserved all morphological parts of a complete flower, they function in this new assemblage as nectar deposits. Ray florets are commonly imperfect and sterile, but function as petals of a true flower.

In Fig. 5 incomplete and imperfect flowers of _Euphorbia_ are surrounded by a flowerlike involucre that imitates a single flower. In _Euphorbia_ _splendens_ Bojer (A) these pseudo-flowers are dimerous, but in _E._ _corollata_ Engelm. (B) they are pentamerous. Actual flowers are unisexual but a cyathium contains both staminate (C) and pistillate (D) flowers. After anthesis only pistillate flowers develop into fruits (E).

Further types of pseudo-flowers are pictured in Fig. 6. In _Poinsettia_ _pulcherrima_ Grah. (A), the true flowers are inconspicuous in the axils of brightly colored upper leaves. In _Cornus_ _florida_ L. (B) large pseudo-flowers are formed from four prominent white bracts that surround the central cluster of flowers.
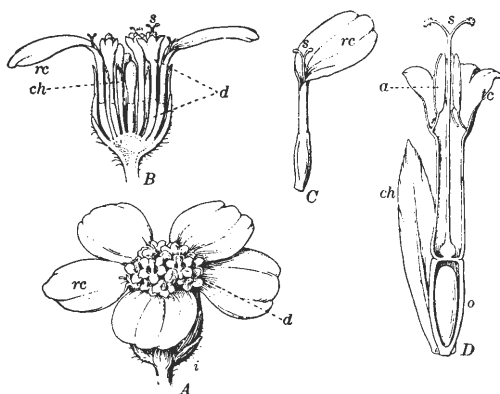
Figure 4.  The flower head (inflorescence of yarrow, <u>Achillea mille-</u>
<u>folium</u> L.   A. The head with exposed rays (rc) and disks (d).
B. Vertical section through the head.   C. a single ray, floret.
D. Vertical section of a disk floret. All greatly enlarged. Expl.:
a = anther; ch = chaff; d = disk floret; i = involucre; o = ovary;
rc = ray floret; s = stigma; tc = tubular corolla.  (Courtesy of
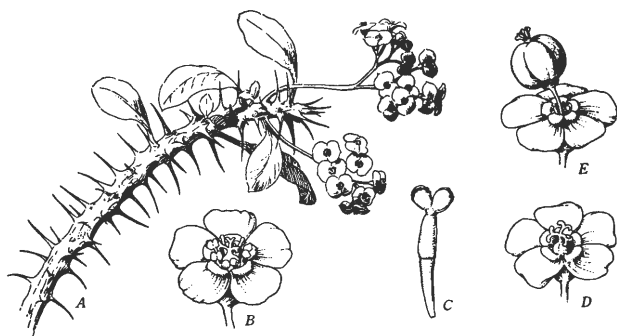Ginn and Company, New York.)



Figure 5.  Incomplete and imperfect flowers (cyathium) of <u>Euphorbia</u>
<u>splendens</u> (Bojer (A) and <u>E</u>. <u>corollata</u> Engelm. (B).
A. A flowering twig showing numerous flower clusters (cyathia)
each of which resembles a cimerous single flower.  B. an inflor-
escence (cyathium) looking much like a pentamerous single flower.
C. A staminate flower from B.   D. the involucre after removal
of staminate flowers from B.    E. the inflorescence after pistil
has developed into a young fruit.  (Courtesy of Ginn and Company,
New York.)
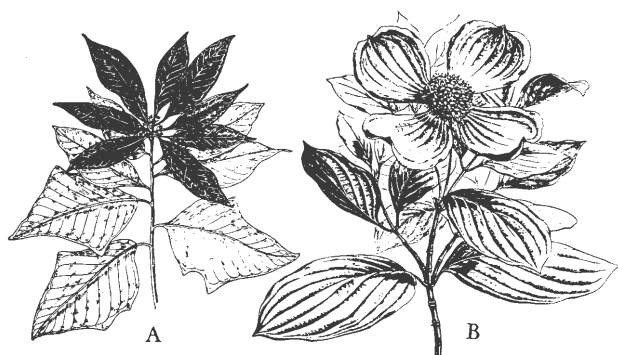
Figure 6. Pseudo-flowers of Poinsettia (A)(dark in figure)that are bright
red upper leaves, and flowering dogwood, Cornus florida L. (B),
with tetramerous pseudanthium composed of bright white bracts.
(Courtesy of Ginn and Company, New York.)

Evolution of such pseudo-flowers cannot be explained with morpho-
logical terms and present workers again tend to put more emphasis on
the physiognomic nature of the flower (Thompson, 1944; Sprague, 1962).
Arber (1937), Emberger (1944), and Lam (1948, p.135), for instance, in
attempting to arrange the generative organs of angiosperms into a new
morphological system, concluded that a "flower, even the most simple
one, is not a morphological unit, but rather a physiognomic and biologi-
cal conception." Barnard (1961) recently proposed considering sepa-
rately the aspects of a flower as a morphological unit and as a biological
entity.

Some of the main obstacles that hinder correlation of morphological
concepts with ecological principles are the manifold functions of a flower.
It is actually a very special shoot-system adapted to perform a whole
sequence of reproductive functions, including advertising, pollination,
fertilization, and dispersal of fruits or seeds. Every one of these func-
tions requires a special arrangement of particular organs, all united
into a single system functioning as a definite whole (Table 1).

Table 1.    Comparative list of successive stages of flowering plants
(according to Leppik, 1961a, p.18).

| Shoot systems | Stages | Functions | Arrangements |
|---|---|---|---|
| Foliage | vegetative | photosynthesis | phyllotaxis |
| Sporophylls | anthetic | reproduction | anthotaxis |
| Semaphylls | pollinative | advertising | semataxis |
| Carpels | fruiting | dissemination | carpotaxis |

After the long and fundamental development of morphological concep-
tions of the phylogenetic origin of various flower parts, it seems advis-
able to maintain these terms in their proper morphological meaning,
and to introduce some new concepts for the functional characterization
of the flower. The term "semaphylls" (Leppik, 1956, p.452) seems ap-
propriate to indicate the basic functional difference between showy parts
in a flower and its reproductive organs, called "sporophylls." Sema-
phylls[6] are mainly nonreproductive structures such as petals, petaloid
sepals, staminodia, colored bracts, and upper leaves. Sometimes
brightly colored stamens or pistils fulfil the function of semaphylls.

Prantl (1888) introduced a functional term "honey-leaves" or "meli-
phylls" for nectar-producing phylloid organs in the Ranunculaceae. More
recently this term was replaced by "nectar-leaves" or "nectarophylls,"[7]
to distinguish nectar from honey. Accordingly, a "nectar-leaf" can be
defined as any phylloid organ that bears nectaries (nectar-secreting
glands, frequently as protuberances, scales, cups, or pits).

In a previous paper (Leppik, 1961a), an attempt was made to corre-
late the floral arrangement with the well-studied foliage systems and to
derive some new terms for floral orders from the classic phyllotaxis
concept. In this terminology, the arrangement of semaphylls (showy
parts of flowers) was called semataxis[8]; that of the sporophylls (genera-
tive organs), anthotaxis; and the arrangement of fruits (or seeds), car-
potaxis (Table 1).

Thus, a complete series of new technical terms is gradually intro-
duced by anthoecologists to define the main phases and functional devices
in the process of pollination (Table 2). These terms help to eliminate
former contradictions with the morphological conceptions. This new
classification is most useful for the evolutionary study because any one
of these orders, semataxis, anthotaxis, and carpotaxis, has its own
hologenetic trend of evolution, and may be analyzed separately.

In this paper, only the sematactic evolutionary trend of showy flowers
is considered. The evolution of generative floral parts, particularly the
development of seed-bearing structures in various geological periods, is
described by Thomas (1936).

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[6] Semaphylls are described in a previous paper (1956a) as "food marks,"
or "trophosemeions," of pollinators which guide visitors to their food
plants. In contrast to "sporophylls" which are stamens and pistils of
ordinary flowers, semaphylls are formed from petals, sepals, stami-
nodia, bracts, or colored upper leaves. Semaphylls and trophoseme-
ions are different from "nectar guides," which are special pointers of
nectar deposits in flowers.

[7] Nectarophylls or "nectar-leaves" ("honey-leaves") are vestigial petals
or stamens in the Ranunculaceae that bear nectar-secreting glands.

[8] Semataxis is a new term introduced by Leppik (1961, p.4) for the sys-
tem of semaphylls, the special "food marks" or trophosemeions of
anthophilous insects. These marks are the showy parts of the flower,
such as the petals and colored sepals in ordinary flowers; but also
petaloid stamens, colored spathes, bracts, white involucres, anthoid
inflorescences, and the discolored upper leaves of many pseudanthous
plants, which serve as trophosemeions or food marks for anthophilous
insects.

Table 2.   Comparative list of morphological and typological (functional) terms in flowering stage of angiosperms.

| Flowering plants | Morphological terms | Typological terms |
| --- | --- | --- |
| Unshowing flowers of aphananthous plants | pistils<br>stamens | megasporophylls<br>microsporophylls |
| Showing flowers of phaneranthous plants | staminodia, petals-corolla<br>sepals-calyx, bracts | nectarophylls<br>semaphylls |

In regard to the mechanisms of pollination, two main trends can be distinguished in floral evolution; the biological trend of entomophilous (and zoophilous), and the mechanical trend of anemophilous plants. Entomophily results in progressive development of the showy parts of flowers while anemophily results in regressive development of these parts.   One can call the first group "showy flowers" of "phaneranthous" plants, as opposed to "unshowy" blossoms of "aphananthous" plants. Both terms: ἀφἄνάνθος,   φἄνεράνθος, are derived from Greek, as follows: φἄνερός   , visible; ἄνθος   , flower; ἀφἄνης   , invisible.

Accordingly, phaneranthous plants bear showy "flowers" in the original, historical meaning of the word.   These flowers are composed of sporophylls (stamens and pistils) and semaphylls (petals, sepals, tepals, bracts, upper leaves, or any other showy part which serves to advertise the flower to pollinators), and are visited by insects, birds, bats, or any other animal looking for food in flowers.   Aphananthous plants, on the contrary, bear mostly anemophilous flowers without semaphylls.

During anthesis, semaphylls are arranged in a definite pattern which functions as a trophosemeion or "food mark" for pollen- or nectar-seeking pollinators.   Their evolution, therefore, must necessarily be correlated with the sensory development of contemporary pollinators, particularly with the ability of these pollinators to distinguish flower patterns. Consequently, the evolution of showy flowers must necessarily follow a natural sequence from the primitive and elementary forms to more specialized patterns as described elsewhere (Leppik, 1953b, 1957b) and pictured in Fig. 1 of this paper.

FLORAL MORPHOLOGY AND MERISTIC VARIATION[9]
IN THE RANUNCULACEAE

Typical flowers of admittedly primitive ranalian genera are regularly bisexual, with complete perianth, and predominantly with numerous

[9] Meristic variation is the differentiation of flower parts to dimerous, trimerous, tetramerous, pentamerous, hexamerous, decimerous, oligomerous, or polymerous structures.   Progressive floral evolution is characterized by gradual reduction in the number of flower parts, from polymerism to oligomerism, to pentamerism, trimerism, and so on.

spirally arranged sporophylls around a central axis. Such an elementary
floral structure has many similar features with the haplomorphic mag-
nolian prototype and can be readily derived from the hypothetical antho-
strobilus of Arber and Parkin (1907-1909). This structure also can be
connected with the gonophyll branch system of Melville (1960, 1963),
which presumably has preceded the flower cone of magnolia. Advanced
genera, on the contrary, are characterized by gradual reduction in the
numbers of floral organs from polymerism to pleomerism, by replace-
ment of spiral divergences in flower parts with cyclic orders, and by a
progressive differentiation of semaphylls (Fig. 3).

Trapl (1912, p. 279) summarized available evidence indicating why
spiral and acyclic flowers in the Ranunculaceae have to be considered as
primitive and cyclic arrangement as progressive. All gymnosperms are
acyclic, and are doubtlessly older than angiosperms. Lower angio-
sperms, such as Magnolia, are basically acyclic but show a clear ten-
dency to cyclic perianth arrangement.

Calycanthus, another relative of the Ranunculaceae, has a cyclic
arrangement throughout. Bisexual, fragrant flowers here have all the
characteristics of a haplomorphic type. The spirally disposed perianth
is composed of numerous imbricated tepals (semaphylls), undifferentiated
into sepals and petals, 5-30 stamens, and gynoecium with about 20 dis-
tinct pistils, situated within a cuplike receptacle (see Fig. 8:7). Illicium
(fam. Illiciaceae) has typically actinomorphic flowers with 7-33 tepals,
numerous stamens, and with 7-15 (21) pistils (Fig. 8:1). In the Ranun-
culaceae, all intermediate stages are represented, from the acyclic
primitive flowers to the exclusively cyclic floral arrangement in the
higher angiosperms.

Such is also the general trend of floral evolution from the general and
more elementary types toward specialized floral structures (Fig. 1).
This sequence corresponds to the sensory development of pollinating
insects (Leppik, 1957b). It appears in a most logical order, evolving
from the indeterminate, general beginning to more and more specialized
forms derived from the undifferentiated types (Däniker, 1959).

## Stamens and Carpels

Stamens and carpels, i.e. the sporophylls in sensu lato, are phylo-
genetically the most constant flower parts in the Ranunculaceae. They
are essential for sexual reproduction, and, therefore, must be present
in every fertile flower, regardless of its phylogenetic origin. Even if
the angiosperms evolved from some anemophilous or sporophorous
ancestors, as postulated in the conventional strobiloid and gonophyll
theories, the micro- and megasporophylls must have already been pres-
ent in that early stage of development.

In primitive flowers, the stamens and pistils are numerous and spir-
ally arranged around a central axis. Commonly, both sexes are present
in the same flower or in different blossoms in the anemophilous plants.
During the progression of entomophily in the higher flower types, the
number of sporophylls has been gradually reduced to pentamery, trimery,
or a single unit. In the Ranunculaceae high numbers of stamens and car-
pels, accordingly, prevail in more primitive genera, such as Anemone,

Ranunculus, Caltha, Paeonia, but this number is drastically reduced in advanced genera, such as Delphinium, Aquilegia, Isopyrum, Cimcifuga, and Actea. The pentamerous flowers of Aquilegia, for instance, contain five carpels and stamens, or multiples of five, with the most common number being 45 or 40 (Tepfer, 1953, p. 527).

## Bracts and Sepals

In the Ranunculaceae, the outer perianth, composed of bracts and sepals, has predominately a foliar character (Trapl, 1912). Smith (1926), Salisbury (1931), Wilson and Just (1939), and Tepfer (1953) have brought both anatomical and morphological evidence to support this view. The transformation of cauline leaves into bracts and of bracts into sepals are demonstrated in the closely related genera Anemone, Hepatica, and Pulsatilla. Here the process itself seems to be secondary and tends to replace morphological sepals, which took over the function of petals. The long pedicels of Anemone obviously serve to protrude the flowers from the bracts and from green foliage and thus heighten the effect of corolla.

The arrangement of perianth leaves is primarily spiral, but tends to become cyclic in higher levels. Cunnell (1958) established that the quincuncial calyx of Ranunculus repens L. is a direct continuation of the spiral from the prophylls. Salisbury (1919, 1931) found the same sequence in R. parviflorus L., Eranthis hyemalis (L.) Salisb., and Ficaria verna Huds. Originally, the purpose of bracts and sepals undoubtedly was the protection of inner flower parts, until a new function arose to heighten the effect of showy parts in a flower with additional semaphylls. This new function must necessarily have evolved in correlation with the sensory development of contemporary pollinators.

## Petals, Nectar-leaves and Semaphylls

Petals are the most changeable parts in ranalian flowers. They vary in color, shape, and size, but differ morphologically in diverse genera. This morphological instability of petals can be explained by the late appearance of corolla in the phylogenetic history of angiosperms, definitely not before this plant group was involved in insect pollination. But even in their later history, petals have the most uncertain position, becoming nectar-leaves (Delphinium, Aconitum), being replaced by sepals (Ranunculus) or disappearing entirely in the anemophilous flowers (Thalictrum). Petals originally served as semaphylls to attract pollinators, a function which was later transferred to many other parts of the flower.

As late comers in the phylogenetic history, petals do not possess their own phylogenetic primordials, but are formed secondarily from some other flower part already in existence. Goebel (1933) explained the late appearance of petals in the ontogeny of the flower with their status as arrested stamens, which view was supported by de Candolle (1813), Troll (1928), Arber (1937), and many later investigators. The foliar origin of the petal, in spite of its dorsiventrality and laminar form, is less obvious. However, according to Goethe (1790), the stamens themselves are but metamorphosed leaves.

Just as variable is the number of petals, which varies from genus to genus, or even, in some genera, from species to species. More primitive genera commonly possess flowers with many petals, the number frequently varying among individuals. On the contrary, in advanced flowers there is tendency toward reduction of the number of petals to a definite number, such as 8, 6, 5, 4, and 3. This number tends to be fixed in all individuals of the same species. Table 4 and Fig. 12 show some selected examples of statistical counts from the available material.

## PHYLOGENETIC CLASSIFICATION OF THE RANUNCULACEAE

Phylogenetically, the Ranunculaceae form a natural group composed very likely of closely related genera. Prantl (1891) divided this family into three tribes, which were raised by Janchen (1949) to the rank of subfamilies. These three subfamilies are Paeonoideae (including phylogenetically uncertain genera **Glaucidium** and **Hydrastis**), Anemonoideae (characteristic by uniovulate pistil), and Helleboroideae (multiovulate pistil). Current phylogenetic and cytologic studies of Ulbrich (1905-1938), Wordsell (1908), Schrödinger (1909), Rassner (1932), Schöffel (1932), Wodenhouse (1936), Brouland (1936), Stern (1946), and others, support such phylogenetic grouping. Gregory (1941), for instance, found that **Paeoniae** with **Glaucidium** and **Hydrastis** contain large chromosomes of 5X, **Anemonae** large or small of 7X or derivatives, and **Helleborae** 8 chromosomes or derivatives from this number (Fig. 7). Only the very small chromosomes of **Coptis** and **Xanthorhiza** with basic number = 9 did not match well with other groups. Extensive systematic serological studies in the Ranunculaceae were made by Hammond (1955).
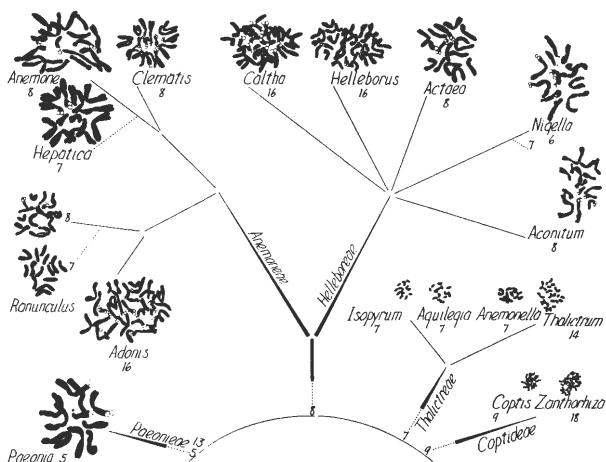


Figure 7.   Chromosome types and groupings in the Ranunculaceae according to Gregory (1941).

The phylogenetic splitting of the ancestral Ranunculaceae obviously took place very early so that the recent tribes and genera have had long evolved side by side before their further splitting into species, sub-species, and smaller units. All this material must have been exposed long enough to the selective activity of food-searching insects, to cause parallel development of flower types in subfamilies and even in many genera (Fig. 13).

## Paeonioideae

The most elementary floral structures, similar to the Magnolia flowers, occur in the genus Paeonia (Fig. 12, Plate 3). More primitive members of this genus possess large flowers with many petals (P. dela-vayi Frachet has 8-9 petals), mostly white, yellowish, or pink. More advanced species, on the contrary, have radiate symmetry with polym-erous or pentamerous corolla. But no trace of stereomorphism or zygo-morphism is known in peony flowers.

This archaic floral structure of the genus Paeonia corresponds to other primitive characteristics, such as shrubby habit of the section Moutan and a marked anatomical affinity with Magnoliaceae. Wordsell (1908), therefore, suggested the segregation of Paeonia as a separate unigeneric family. But this separation, although generally agreed upon, has never become a well established practice because of several other characteristics that bind peonies with the Ranunculaceae.

Barber (1941) and Stern (1946) suggested that Peonies might have arisen in Central Asia, where the primitive shrubby section Moutan is indigenous. But they must already have been distributed in early Ter-tiary throughout the northern hemisphere on Eurasian and American continents. The original area of distribution very likely was interrupted repeatedly during glacial periods. However, the eastern part of Central Asia was free from ice and some members of the present section Moutan such as P. suffruticosa Andrews, P. delavayi Franchet, P. lutea Delavay and P. potanini Komarow may be direct descendants from ancestors which might have survived all glacial periods. As mentioned above, this section is characterized by archaic shrubby habit, diploidy, large mag-noloid flowers, and magnoliaceous wood anatomy. The North American section Onsepia, with two diploid species, seems to be distantly related to this Asiatic section.

It is further suggested that the European peonies have been moved down to the Mediterranean islands and into other warmer areas by in-creasing glacial pressure from the north. Descendents of these pre-glacial diploid species are living now in various Mediterranean and Caucasian areas. Some of them, however, have later produced tetra-ploid forms with high vitality and large areas of distribution.

Presumably, the genus Paeonia is not only an important phylogenetic link between primitive woody angiosperms and more advanced herbace-ous Ranunculaceae, but also connects the sequence of floral evolution with primitive Magnolia flowers. Very likely both magnolias and peonies have been long exposed to the selective activity of the same insect groups (assumably beetles) which preferred to visit flowers with haplomorphic characteristics. Although haplomorphic flowers are accessible to many

insect groups, beetles are the predominant visitors of both magnolias
and peonies even today.

Hydrastis and Glaucidium are more advanced phylogenetically and
possess trimerous or pentamerous flowers of pleomorphic type-class
(Bowers, 1891).
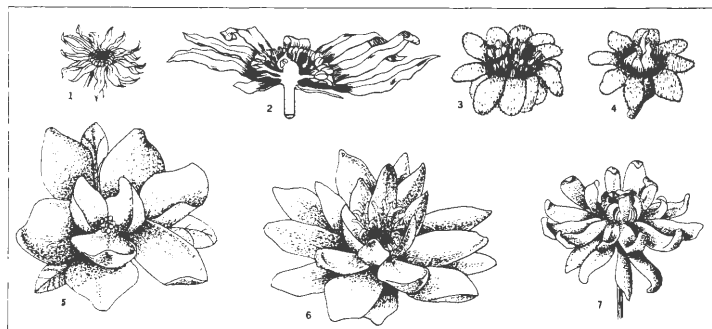


Figure 8.  Haplomorphic and actinomorphic flower types in ranalian
     plexus.  1. Illicium floridanum Ellis.  2. Vertical section from 1.
     3. Boldea boldus Perk. staminate flower.  4. The same, pistillate
     flower.  5. Magnolia grandiflora L., haplomorphic flower.  6. Nym-
     phaea alba Prsl. flower.  7. Calycanthus floridus L., flower.
     Redrawn from pictures (by Bailey) and photographs.  Pictures 1-4
     courtesy of Macmillan Company.

Anemonoideae

The subfamily Anemonoideae contains representatives of actino-
morphic and pleomorphic type-classes and some genera with secondarily
reduced flowers (Thalictrum,  Myosurus). In the genus Anemone,  both
actinomorphic  (A. apennina, A. coronata) and pleomorphic (most spe-
cies) are represented.  Other genera are predominantly pleomorphic,
containing flowers with 8, 6, 5, or 4 petals, or petaloid sepals (Britton,
1892).  For comparison see Plates 5, 6, 9, 10, 12, 13, and 14.

A small subtribus Kingdoniinae with two genera, Kingdonia and Cir-
caeaster, from China represent an isolated plant group with clearly
ranalian characteristics.  Janchen (1949, p.44) joined these plants with
the tribus Clematideae of the subfamily Anemonoideae.  Although these
monotypic genera are undoubtedly angiosperms and are affiliated with
the Ranunculaceae, the dichotomous venation pattern of their leaves
strikingly resembles the venation pattern of Ginkgo biloba L. and certain
ferns (Foster, 1959).

## Helleboroideae

In this subfamily, both progressive and regressive trends of floral evolution are represented in several genera. Aquilegia, with its long spurs (progressive trend), is a stereomorphic type. These flowers are unique, because every petal forms a long spur, imitating a compound flower. A. ecalcarata Maxim. from Asia, with the most poorly developed spurs is, according to Munz (1946), primitive. American species of Aquilegia are accordingly considered by Payson (1918) to be progressive. Delphinium, on the contrary, has a single spur. Aconitum has a typically zygomorphic flower (Gayer, 1909; Ewan, 1936, 1945; Munz, 1945). Trollius europaeus L. shows a regressive trend in its floral differentiation, having formed secondarily a haplomorphic (spheric) flower from an actinomorphic corolla (Shipczinsky, 1924). Floral structures of Delphinium, Aquilegia, and Aconitum, see Plates 15, 16, 17, and 18.

## EVOLUTION OF FLOWER TYPES IN THE RANUNCULACEAE (Fig. 13)

Prevailing entomophilous characteristics, such as bisexuality, nectar-secreting glands, and indigenous showy flowers of the Ranunculaceae unmistakably point to the early involvement of this family in insect pollination. Occasional reduction of showy petals and unisexuality in some species of the genera Thalictrum and Cimcifuga are obviously a secondary adaptation of this genus to wind pollination, predominantly very likely because they occur in open grassland areas, which are sparsely populated by pollinating insects. Anemophily, however, is not the sole mode of pollination in Thalictrum. Intensively colored showy stamens of several woodland species in this genus attract bees, beetles, and other pollen-eating insects, which carry pollen from flower to flower and from plant to plant. Parthenogenesis occurs in some species.

One can assume, therefore, that the ancestors of the present-day Ranunculaceae already were entomophilous and that floral evolution in this family took place concurrently with sensory development of their pollinators through several geological periods. This view is in agreement with conventional theories that the early angiosperms were entomophilous and that pollinating insects may have been a significant agent in the evolution of flowering plants (Robertson, 1904; Neumayer, 1924; Parkin, 1951; Nemejc, 1956; Boughey, 1959; Axelrod, 1960, p. 243, footnote, and 1961, p.456; Eames, 1961). In these circumstances, the extreme diversity of flower types in such old and large families as the Ranunculaceae appears natural and seems properly adapted to the sensory environment of their progressive pollinators.

Birds and other animals seemingly have been less actively involved in the evolution of the Ranunculaceae. There are only a few truly ornithophilous flower types in the ranalian plexus, such as Aquilegia canadensis L. and Delphinium tricorne Michx., and all occur in the higher evolutionary levels. In North America, for instance, all ornithophilous Ranunculaceae are visited according to Robertson (1928), by Trochilus colubris L. This fact indicates the comparatively late appearance of birds among the pollinators of this family.

## Pre-Ranalian Flower Types

From other sources (Leppik, 1960b, 1962, 1963a, 1963b) it is known that elementary flower types occurred among mesozoic Cycadophyta long before the first appearance of angiosperms in paleontological records. Numerous well preserved fossils of cycadeoid flowers reveal their essential entomophilous characteristics, such as bisexuality, occasional protandry, well-developed semaphylls, perfect floral shape, and exquisite symmetry. Beyond doubt, such elementary but morphologically well-perfected flowers must have had some color, presumably white or yellow, in contrast to the green foliage. Very likely these early flowers were adapted to the elementary sensory abilities of their contemporary pollinators, precominantly beetles, which were conditioned to distinguish and remember such primeval flower types in the pre-Cretaceous floras (Leppik, 1960b).

The early development of cycadeoid flowers must have enabled many phytophagous insect groups to become conditioned to these elementary types and gradually to acquire an inherited ability to distinguish and remember elementary floral characteristics. In the Mesozoic era, during the expansion of beetles, amorphic, haplomorphic and actinomorphic flower types became common among some Cycadophyta. In recent floras these types occur in most diverse groups of angiosperms, but their principal visitors are still beetles. At the same time, many modern flower types have evolved in correlation with the sensory development of higher pollinators to a remarkable diversity and specialization.

Conclusive evidence deduced from fossil records indicates that the pollinating insects must have lived with some gymnospermous flowers (mainly Bennettitales) about 100 million years (roughly estimated) before they met early angiosperms (Leppik, 1960b). Accordingly, this long "experience" and some elementary level of their sensory development permitted these insects to recollect quickly (in a geological sense) floral characteristics that were already engraved in their innate memory as definite senses for form and symmetry. Consequently, the long pre-angiospermous existence and wide distribution of elementary flower types among Cycadophyta explains the instantaneous appearance and rapid increase of well-perfected type-classes[10] in the early ranalian plexus.

## Early Ranalian Flowers

In the light of recent investigations, it seems reasonable to assume that the early Ranales, no matter where or when they first appeared on the scene, already must have been surrounded by a diversity of pollinating insects. A considerable number of these insects must have at that time reached in their sensory development a certain elementary level to

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[10] Type-class is defined in some previous papers (Leppik, 1957b, footnote) as a group of flower types of the same evolutionary level with similar principal characteristics. So far those described are amorphic, haplomorphic, actinomorphic, pleomorphic, stereomorphic, and zygomorphic type classes.

distinguish and remember primitive flowers of amorphic, haplomorphic and actinomorphic types that were common for both flowering Cycadophyta and early angiosperms (Leppik, 1960b). Fossil evidence indicates that these insects were assumably beetles, flies, stoneflies, bugs, wasps, and thrips, which hitherto have lived and evolved with flowering Cycadophyta. Frequently fossilized parts of these insects are found in the same beds with plant remnants.

This explains the striking resemblance of cycadeoid flower types to those of primitive Ranunculaceae in the haplomorphic and actinomorphic levels. It is possible to interpret the floral convergency in many phylogenetically unrelated plant groups as a result of selective or trophectectic activity of insect pollinators that are guided by their long established innate senses.

In Figure 8 are shown some early ranalian flowers with primitive entomophilous characteristics. Pictured are: Illicium (Fig. 8:1, 2), Boldea (Fig. 8:3, 4), Magnolia (Fig. 8:5), Nymphaea (Fig. 8:6), and Calycanthus (Fig. 8:7). Haplomorphic form is prevalent in these flowers with a marked tendency to expand radiate symmetry when in full bloom.

Representatives of the first amorphic level have not survived among the present-day floras, but some haplomorphic types still occur among the living Ranunculaceae. It is possible, therefore, to begin with the haplomorphic level and to follow the whole evolutionary sequence on living material. Our next question, consequently, is why amorphic flowers evolved to haplomorphic and actinomorphic types, although all three are equally accessible to, and are actually visited by, all insect groups with more elementary senses for form and symmetry.

The early phylogenetic splitting of ancestral Ranales into smaller groups must have created a parallel development of many genetically isolated taxa, all exposed to a diverse population of pollinators. This genetic partition also must have produced some variation in flowers, such as size, color, form, odor, and possibly primitive nectar deposits. Thereafter, it became important for plants to avoid the mixing of incompatible pollen of these new taxons. Insects, on the other hand, urgently needed distinctive characteristics for their food plants as soon as these began to differ in food qualities and quantities, such as pollen, nectar, and edible parts of flowers. Thus, a further differentiation and mutual specialization became both an indispensable necessity for plants and an obvious advantage for insects. But it must have been the selective activity of pollinating insects, correlated with their increasing ability to recognize and memorize floral characteristics, that accelerated the further floral evolution of the Ranunculaceae and other angiosperms.

There is a natural tendency of haplomorphic flowers in full bloom to spread their petals (semaphylls) in a radial level (Fig. 8). Such simple rearrangement of semaphylls strengthens the visual effect of flowers from distant view and makes it easier for visitors to find their food in the differently colored central part of the floral disk. An obvious advantage for plants in this rearrangement is better attraction of insects and the possibility of conducting visitors directly to the pistils and stamens, which are assembled in the central part of the flower. An advantage of haplomorphic flowers, however, is that between their concave petals they can offer better protection to insects looking for shelter. For

instance, Paeonia potanini Komarov (Plate 3:1) and Trollius europeus L.
(Fig. 9:2) are used by many small insects as shelter.

The remarkable tendency for haplomorphic flower types to resolve
their hemispheric shape into a radiate actinomorphic pattern has been a
common trend in the archaic flowers of the Bennettitales and Cycadeo-
ideae, as is shown in the paleontological records of these plants (Leppik
1960b, 1963a). A similar trend was exhibited in the floral differentiation
of the lower Ranunculaceae and is furthermore demonstrated in numer-
ous special cases among the present-day angiosperms. Consequently, a
progressive haplomorphic type tends to develop into an actinomorphic
form, if visited by progressive pollinators, or to stay unchanged if pol-
linated by unskilled insects. Examples of both cases are numerous. In
the successive development of the peony flowers, for instance, all inter-
mediate stages can be observed, from a strictly haplomorphic type to a
perfectly actinomorphic pattern, frequently exposed in the same flower
during its ontogenetic development (Plate 3:1-2).

It is appropriate to mention here that the corresponding human judg-
ment upon form and symmetry is relatively less conditioned to floral
patterns than are the inherited senses of many hymenopterous pollinators.
To the human eye, for instance, primitive haplomorphic forms appear
more pleasing than are the higher actinomorphic and pleomorphic pat-
terns. Still more strange and remote to us are the intimate structures
of stereomorphic and zygomorphic flower types in the highest evolution-
ary level. Hence it appears that most man-bred garden peonies, asters,
daisies, marigolds, and roses are actually regressive trends from some
more advanced wild species (see Leppik, 1961b).

In nature, such regressive trends in floral evolution appear as a
consequence of an exchange of pollinators having less developed senses
than those of the previous insect visitors. In the actinomorphic genus
Trollius, for instance, some species, such as T. europaeus L. and T.
sibiricus Ledeb. have fully restored their archaic haplomorphic shape
and form, as a consequence of their less evolved visitors. Large yellow
haplomorphic flowers (Fig. 9:1) of these species remain closed to bees
and butterflies, but are accessible to small flies that crawl inside be-
tween carpels and stamens (Fig. 9:2). Small insects prefer to stay in-
side of haplomorphic flowers where they are protected against rain and
wind. During mating season these flies are carrying pollen from flower
to flower, selecting for this purpose yellow haplomorphic blossoms of
their food plants.

According to Hagerup (1959, p.231), T. europaeus L. is pollinated
by a little black fly, Chiastochaeta trollii Zet., which eats pollen and
lays eggs on the carpels. Larvae eat some seed which are produced
abundantly after successive cross fertilization performed by these flies.
This fly is common wherever T. europaeus grows, from northern Scan-
dinavia to Italy. The plant has been introduced into North America,
where it does not set seed because of the absence of the above-mentioned
fly. Yet some other plants, such as Magnolia and Nymphaea, have pre-
served their haplomorphic flower types as long as 100 million years.

In the sensory development of insects that already are familiar with
the haplomorphic flowers, only a short evolutionary step is necessary
to reach the ability to distinguish and remember an actinomorphic floral
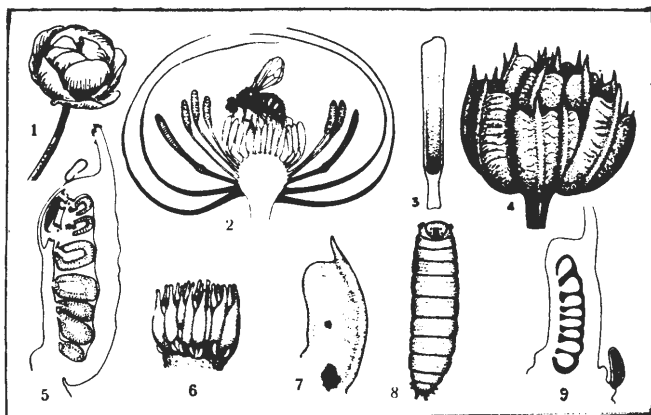
Figure 9.   Trollius europaeus L.   1. Flower.   2. Cross section through
     the flower with a little black fly,   Chiastochaeta trollii   Zett.
     3. Petal with nectar secreted on the upper surface.   4. Fruits.
     5. A larva (black) digging inside of a fruit.   6. Eggs are fastened
     to the young carpel.   7. Damaged ovary,   8. Larva.   9. An egg
     fastened to the young carpel. (According to Hagerup and Petersson,
     1959; courtesy of Munksgaard Company, Copenhagen.)

pattern.   This seems to be the general progressive trend in the sensory
evolution of numerous anthophilous  insects.   Nevertheless, many less-
developed insects do not have the necessary ability in their  sensory
development and, consequently, cannot exercise any selection for pro-
gressive evolution in the actinomorphic level and above.   These insects
either disregard possible mutations with new characteristics or cross
them occasionally with the other varieties until the new symptoms dis-
appear again.

### Progression of Pleomorphism in the Ranunculaceae (Fig. 10)

Because of the continuous phylogenetic splitting and taxonomic parti-
tion among the early Ranunculaceae, new floral characteristics and fur-
ther differentiation of existing types were required for the guidance of
pollinators to the proper plants.   One merely needs to consider the un-
usual diversity and concealment of nectaries among the Ranunculaceae
to realize the importance of distinctive floral characteristics for the
nectar-seeking pollinators. Conversely, haplomorphic and actinomorphic
types alone, in spite of their additional variation in size, color, and odor,
were no longer adequate for the distinction of continuously increasing

number of species among the fast-evolving Ranunculaceae. These pre-
dominantly herbaceous plants expanded rapidly on the vast areas of the
northern hemisphere, providing additional food for the quickly spreading
population of hymenopterous and lepidopterous pollinators. Particularly
the newly emerged aculeate insects, with their higher sensory system
capable of further progression, must have responded to this new chal-
lenge, for they soon became dominant pollinators among the modern
Ranunculaceae.

On the other hand, new gene combinations in a progressive and ex-
panding group, such as the early Ranunculaceae, must necessarily have
produced considerable variation in the existing haplomorphic and actino-
morphic flower types. The splitting of a polymerous actinomorphic type
into several subtypes with definite number of petals, i.e. the progres-
sion of pleomorphism, must have been, therefore, one of the most logical
intermediate stages and connecting links in the floral evolution. There-
after, further progress of pleomorphism obviously has depended on the
choice of pollinating insects, according to which forms of numerous pat-
terns they could easily remember and select for their successive visits.

In these circumstances, the appearance of aculeate insects among
pollinators (early bees, wasps, and bumblebees might have been among
them) might have caused the turning point in the floral evolution of the
Ranunculaceae. In their incessant search for better food plants, these
insects must have noticed the distinctive effect of trimerous, pentamer-
ous, and polymerous flowers, particularly when these characteristics
were associated with food quality and quantity, as they actually are.

Admittedly, the gradual conditioning of the sensory abilities of insects
to the recognition of pleomorphic patterns in flowers was just another
progressive step in the evolution of their senses for form and symmetry.
Yet, to these newly acquired abilities of insects is owed a new and most
peculiar trend in floral evolution, namely, the differentiation of numeral
patterns in flowers, which serve as "iconic numerals" for food-search-
ing insects, [11] as pictured in Plates 5-15.

## The System of "Iconic Numerals" of Insects

Numerical patterns in flowers help nectar-seeking insects to recog-
nize and remember their food plants, and also these patterns frequently
are valuable distinctive characteristics for taxonomists in species iden-
tification. Regular forms of tri-, tetra-, penta-, hexa-, octo-, and poly-
merous symmetry make flowers look clearly different, even when they
have the same color and size (Fig. 10). Field observations show that
most groups of specialized pollinators, such as honeybees, wild bees,
bumblebees, butterflies, and some flies are capable not only of distin-
guishing such numerical patterns in flowers, but also of using them fre-
quently for identification of their food plants. Training experiments with

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[11]
    Iconic numerals (or figure numerals) are the numeral patterns of bi-,
tri-, tetra-, penta-, hexa-, deca-, and polymerous flowers that enable
bees, bumblebees, and other skilled pollinators to locate flowers with
concealed nectar deposits (Leppik, 1956a).
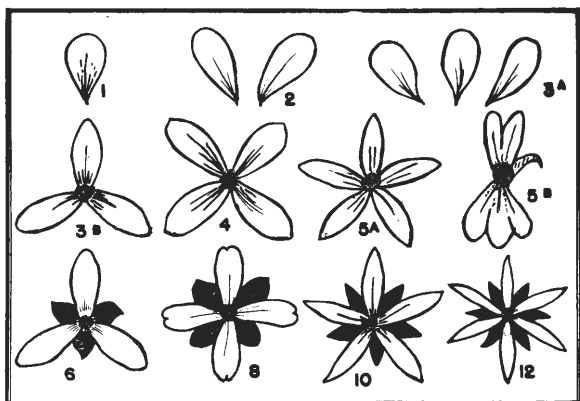
Figure 10.  Symbols of "iconic numerals" in flowers.  They are dis-
tinguishable from one another according to form and summetry
(according to Leppik, 1953b, 1958).

marked bees and tropical butterflies confirmed these observations (Lep-
pik, 1956a, 1956b, 1958).

A further peculiarity of these numerical combinations of flowers is
that they are arranged in symmetrical figures, as pictured in Fig. 10,
and are called, therefore, "Iconic numerals," (also "figure numerals"
in previous papers) to distinguish them from ordinary numbers (Leppik,
1958).  Such simple patterns can easily be distinguished from one an-
other and memorized mechanically, without the ability to count or cal-
culate, even by organisms with a very low level of intelligence, such as
insects.  No wonder, therefore, that most nectar-seeking insects are
conditioned to these numerical patterns in flowers, memorizing them as
definite characteristics of their food plants.  (Compare Plates 9-15.)

### Origin and Development of Pleomorphism in Flowers

Question may be raised as to how the first numerical pattern appeared
in flowers, and why it was attractive to food-searching insects.  As far
as the Ranunculaceae are concerned, the question seems to be not quite
unanswerable.  In this family, the cyclic tendencies prevail in flowers,
accompanied by meristic variation of flower parts (see preceding dis-
cussion).  Salisbury (1919) showed that trimery is a primitive condition
in the ranalian plexus and that pentamerous whorls in highly specialized
zygomorphic flowers are derived from trimerous orders.  In the highly
consistent pentamerous flowers of Aquilegia, Tepfer (1953) found still a
considerable variation in the number of whorls.  The differences appeared

to be caused by genetic factors which produce new combinations and variations.

Thus genetically produced variation in the number of flower parts has a selective value for pollinators as guiding marks for their food plants. Whatever the true morphological origin of every numerical pattern in every special case may be, they all serve the same purpose for pollinators, indicating certain nectar conditions in flowers. Accordingly numeral patterns in flowers present a highly serviceable system for pollinating insects to distinguish their food plants.

According to fossil imprints of flowers, frequently left in sand, mud, or amber, numerical patterns can be traced back until early Tertiary. Later on, in the middle of the Tertiary period, these marks reached the greatest expansion among angiosperms in the northern hemisphere (Leppik, 1964). This must have been the time when the higher pollinating insects acquired the ability to distinguish iconic numerals. In still higher evolutionary levels, however, the numerical patterns are streamlined into zygomorphic structures and thus disappear again from floral pictures (Fig. 1).

### Differentiation of Numerical Patterns in the Ranunculaceae

There are numerous observable trends and intermediate stages among the living Ranunculaceae that represent the gradual differentiation of the numerical patterns from some preceding actinomorphic type. This is actually a simple process of reduction in perianth leaves, which is a common phenomenon in evolution of the Ranunculaceae and other angiosperms. Among the Ranunculaceae, this sequence of reduction is repeated in genus after genus throughout the family, frequently even among species of the same genus. This sequence conforms to the general trend of floral evolution and is recapitulated again and again in numerous families of higher angiosperms. As a matter of fact, numerical patterns occur not only in the Ranunculaceae, where they are fairly well established, but are common even among pseudanthial families, such as the Compositae and Euphorbiaceae.

In the Ranunculaceae, the differentiation of numerical patterns takes place as a parallel development in most genera that have reached the pleomorphic level in their evolution (Figs. 1, 13). The process goes hand in hand with the formation of concealed nectaries. In the lower levels, haplomorphic and actinomorphic types are pollen flowers, or in some cases they secret nectar from inner flower parts. Sometimes such primitive plants may possess elementary "ringnectaries" (Werth, 1941), as in the genus Paeonia. Similarly, other haplomorphic genera, such as Magnolia, Calycanthus, Podophyllum, Nymphaea, Victoria, Adonis, and Anemone (partly), are typical pollen plants with occasional stigmatic or staminal secretion of nectar or with food hairs (Diels, 1916). Pollination of these plants is carried by beetles, one of the most ancient and primitive group of plant pollinators still alive. Concealed nectaries are not known in these plants. Thalictrum, however, is a pollen plant that has reduced its numerical patterns in flowers.

In the oligomorphic Hepatica triloba Chaix. and H. americana B. & B. Rydb. the number of petals varies from 5 to 12, with 6 occurring in the

Table 3. Variation in the number of petals (semaphylls) in pleomorphic flowers. (Total number of analyzed flowers is 1000 in every species.) See Fig.12.

| Species | Number of petals (semaphylls) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
|  | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| 1. Clematis verticillaris DC. | 16 | 903 | 81 |  |  |  |  |  |  |  |
| 2. Anemone canadensis L. |  | 54 | 942 | 3 | 1 |  |  |  |  |  |
| 3. Isopyrum biternatum (Raf.) T & G. |  | 134 | 734 | 106 | 27 |  |  |  |  |  |
| 4. Eranthis hiemalis (L.) Salisb. |  |  | 10 | 826 | 110 | 50 | 3 |  |  |  |
| 5. Hepatica americana (B. & B.) Rydb. |  |  | 3 | 714 | 198 | 58 | 9 | 12 | 4 | 2 |
| 6. Anemonella thalictroides (L.) Spach. |  | 16 | 328 | 356 | 224 | 72 | 4 |  |  |  |
| 7. Ranunculus bulbosus L. |  |  | 10 | 425 | 250 | 125 | 100 | 75 | 0 | 15 |
| 8. Anemone japonica Sieb. & Zucc. |  |  |  | 56 | 821 | 105 | 18 |  |  |  |
| 9. Ficaria verna Huds. |  | 4 | 18 | 118 | 206 | 514 | 88 | 36 | 14 |  |

Table 4. Variation in the number of petals (semaphylls) in actinomorphic flowers. (Total number of analyzed flowers is 1000 in every species.) See Fig.12.

| Species | Number of petals (semaphylls) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
|  | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
| 10. Anemona apennina L. |  | 38 | 82 | 115 | 255 | 137 | 283 | 52 | 28 | 10 |  |
| 11. Adonis vernalis L. | 9 | 21 | 108 | 122 | 140 | 180 | 159 | 143 | 68 | 40 | 10 |
| 12. Anemone caroliniana Walt. | 5 | 16 | 67 | 73 | 86 | 110 | 165 | 210 | 151 | 76 | 41 |
| 13. Anemone decapetala Ard. | 10 | 81 | 39 | 74 | 216 | 282 | 158 | 83 | 37 | 30 |  |

greatest number of flowers (Tables 3, 4; Fig. 12). There is no observable tendency for differentiation of a certain numerical pattern. Since this species is a pollen plant, its numerical pattern would not have any particular value for visitors. This plant blooms in early spring, being almost alone in its habitat, without serious competition at that time of the year. It is visited mainly by pollen-seeking Apidae and Syrphidae, which need pollen at that time of the year, and seemingly have no reason to pick up any particular numerical pattern from those flowers. In these circumstances the plant may long remain in an intermediate stage between actinomorphic and pleomorphic evolutionary levels, in spite of its more advanced genetic systems that already have reached the next higher level in their evolution.

Exposed or partly exposed nectaries in Ranunculus, Batrachium, Myosurus, Caltha, Eranthis, Isopyrum and Cimicifuga are marked with pentamery, tetramery, or hexamery. Completely concealed nectaries of Pulsatilla, Trollius, Helleborus, Atragene, and Nigella are indicated by pentamery or by zygomorphy by Delphinium and Aconitum.

It is, therefore, a great advantage to progressive pollinators to be able to recognize and remember the numerical patterns, that guide them to rich nectar supplies which are inaccessible to less skilled insects. In mastering the system of iconic numerals, skilled pollinators can easily distinguish plants with nectar containers from those that carry pollen, thus knowing in advance what they want and how to get it.

### Numerical Pattern in Pseudanthial Flowers

Some patterns in flower heads of the Compositae are so similar to ranalian patterns that it is often difficult to distinguish one from another. Good (1956, p. 322, fig. 161-162) called attention to the striking similarity between the eight-rayed capitulum of Cosmos bipinnatus Cav. and the octomerous flower of Anemone japonica (Thunb.) Sieb. et Zucc., both common ornamentals (Plate 9). In spite of the fact that the American Cosmos and Japanese Anemone are unrelated genetically and inhabit distant countries, their capitula and flowers are similar in size, shape, and color (both have white and pink forms). Another example is the yellow 5-rayed head of Baltimora recta L., which resembles the flower of Ranunculus. Many other examples are cited in a previous report (Leppik, 1960a). Further examples see in Plates 1, 4-9, 11, 12.

Until recently, the problem of recapitulation of flower types in unrelated families was in a state of great confusion. Good (1956, p. 376), for instance, reviewing all proposed evolutionary theories, including the concepts of orthogenesis, convergency, and mimicry, could not find any reliable explanation for the fact that the most specialized Compositae have "adapted" the floral patterns of the most primitive Ranunculaceae. Further controversies among various authors are commented on and criticized by Pijl (1960-1961) in his recent compendium on floral evolution.

Recent ecologists, however, consider the repetition of flower types in various phylogenetic groups as an ecological convergence, resulting from the selective activity of food-searching pollinators (Leppik, 1960a; Pijl, 1960, p. 404). After all, it seems natural that the cantharophilous

characteristics appear in all plant groups pollinated by beetles; meli-
tophilous, in those pollinated by bees; ornithophilous, in bird-pollinated
flowers, and so on.

## Stereomorphism

On the pleomorphic level a new trend soon became apparent that
caused a further important evolutionary change both in ranalian flowers
and in the sensory development of pollinating insects. Concealment of
nectar supplies in deep tubular cups must have excluded short-tongued
insects from the process of pollination while favoring long-tongued visi-
tors. Such segregation among pollinators evidently stimulated proboscis
development, and gradually long-tongued groups appeared among butter-
flies, bees, moths, and flies. But this specialization among pollinators
likewise must have favored the development of stereomorphic flowers,
which thereafter became well established and widely distributed among
the Ranunculaceae.

Here again we have a good example of mutual interrelationship be-
tween insects and plants, both being reciprocal selective factors in evo-
lution. Obviously the stereomorphic evolutionary trend was even more
effective than the application of numerical patterns on the pleomorphic
level. As a matter of fact, stereomorphic types evolve further into
zygomorphic types, whereas the numerical patterns disappear in higher
evolutionary levels. (Compare Plates 15, 16, and 17.)

## Zygomorphism

The first truly zygomorphic flower in the Ranunculaceae is in Aconi-
tum, with Aquilegia and Delphinium being stereomorphic predecessors
to the zygomorphism. The evolutionary status of these genera, therefore,
has much interest in itself and is of particular significance because it
marks the beginning of a new zygomorphic trend in the evolution of
flower types, and a new stage in the sensory development of pollinating
insects. At that stage of development, several progressive groups of
insect pollinators must have adapted themselves to an entirely new situ-
ation in flowers. In zygomorphic types, nectar is not offered openly any
more, as it is in the earlier actinomorphic and pleomorphic flowers, but
is hidden in some remote corner of the "floral parlor."[12] Although the
monkshood flower is open to all insects, not all visitors in the parlor
can locate and reach the nectar deposits hidden in coiled nectaries. In
flowers having still higher levels of zygomorphism, such as snapdragons,
floral parlors remain closed to most visitors, and are accessible only
to special pollinators that are capable of opening the entrance to the
parlor. (See the bumblebee entering into "parlor" in Plate 19.)

This new situation, having a definite advantage for both partners,
must have stimulated further specialization. The effort of specialized

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[12] "Parlor" is a "reception room" for floral visitors in a zygomorphic
flower. It has a landing place, entrance, guiding signs to nectar deposits
and other accommodations for welcomed customers. But it is frequently
closed for unwanted visitors. (See Plates 18, 19.)

pollinators to search for and locate the hidden nectaries is rewarded by full cups of concentrated nectar, untouched by other visitors. Similarly, plants with specialized flowers have the advantage of having their pollen carried by skilled pollinators to the same plant type, which is not always so in the case of unskilled visitors.

Many higher groups of pollinators, such as bees, butterflies, and some flies, progressed enormously in their sensory abilities to distinguish more and more complicated flower types. Other insects, on the contrary, remained in their archaic level of sensory capabilities. Beetles, for instance, although at one time most important flower "breeders," never have learned to operate the modern pollination systems in zygomorphic flowers, such as in the Orchidaceae (Plate 24).

It is appropriate to mention here that the Aconitum flower is a rather elementary structure among higher zygomorphic flower types such as snapdragons, beardtongues, foxgloves, and others. There are neither variegated colors nor visual nectar guides in the Ranunculaceae. Lex (1954) and Aufsess (1960) found no visual nectar guides among the Ranunculaceae, but more intensive odors in the central parts of flowers in some species. Ranunculus acer L., however, radiates from the central part of the flower ultraviolet rays, to which the insect eye is sensitive.

In these circumstances, it would be highly desirable to establish the first appearance and successive development of the monkshood type and to find the place of this important event in the geological time table. Direct approach to the problem is hindered because of an almost complete absence of paleontological records about the early Ranunculaceae. Nevertheless, some reasonable guesses about the age of Aconitum can be made from the present-day geographical distribution of this genus. Kronfeld (1890), Huth (1895), Rapaics (1908-1910), Diels (1916), and Wilde (1931) consider the genera Aquilegia, Delphinium, and Aconitum to be of Tertiary age. Their circumpolar distribution must already have been completed before the Pleistocene glaciations. During the ice age, however, the original area was repeatedly interrupted and the plants driven southward until they finally reached their present-day distribution in Asia, Europe, North Africa, and North America.

There is no trace of the above-mentioned genera in Australian, South African, Antarctic, and other Gondwana floras, which are considered older than the northern Arcto-Tertiary flora. Yet in the Ranunculaceae, several older genera with actinomorphic flowers, such as Ranunculus, Anemone, Caltha, Clematis, Batrachium, and Myosurus, have reached an almost cosmopolitan spread.

One can assume, therefore, that the zygomorphic types began to differentiate from their stereomorphic predecessors sometime in the early Tertiary period and that they became well established in the Ranunculaceae before the beginning of Pleistocene glaciations. Persistent selective agents for the development of monkshood type obviously have been the Apideae, possibly the ancestors of present-day bumblebees. The present-day area of distribution of the genus Aconitum matches well the distribution of bumblebees except in South America (Fig. 14). Gradual differentiation of zygomorphic types from pleomorphic pattern is demonstrated on Cymbidium and Epidendrum flowers in Plate 24.

## NECTAR-PRESENTATION MECHANISMS IN THE
## RANUNCULACEAE (Fig. 11)

In the Ranunculaceae, the mechanisms involved in the presentation of nectar to insect visitors are as varied as are the devices that produce the sugary fluid. They have been studied by several investigators and are described by Sprengel (1793, 1811), Müller (1883), Kronfeld (1890), Knuth (1908), Brown (1938), Werth (1941), Janchen (1949),  Leinfellner (1958), and others.
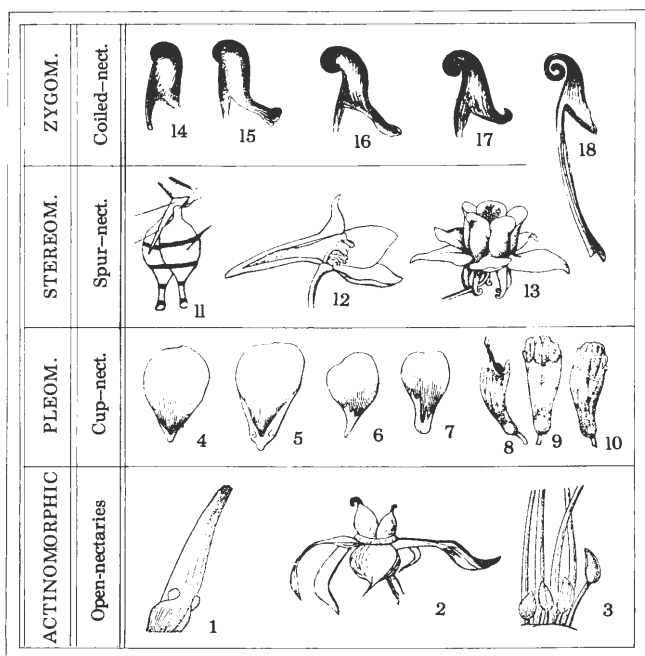


Figure 11.  Evolution of nectar-leaves in the Ranunculaceae.  Open nectaries of haplomorphic and actinomorphic flowers: 1. Caltha, nectar droplets secreted by the carpels; 2. Ring-nectaries of Paeonia; 3. Pulsatilla, vestigial stamens secrete nectar.  Cup-nectaries of pleomorphic flowers: 4-7 Ranunculus, 8-10 Isopyrum. Spur-nectaries of stereomorphic flowers: 11. Concealed nectaries of Nigella;  12. Spur of Delphinium; 13. Spurs of Aquilegia. 14-18. Development of coiled nectaries in Aconitum.

In primitive flowers, sugary fluid as a low-grade nectar may be secreted from almost any floral organ and accumulates mainly in the base of flowers as in Chimonanthus, Asimina and other genera. Paeonia has primitive "ringnectaries" in the flower base and in addition secretes sugary fluid from the sepals.   Stamens are the source of nectar in Pulsatilla; filaments, in Atragene; carpels, in Caltha.  Usually petal-like staminodes bear nectaries at their base (Ranunculus, Batrachium, Myosurus), at their middle part (Trollius), or at coiled tips (Aquilegia, Delphinium, Aconitum).  However, many pollen-producing Ranunculaceae secrete no nectar at all (Clematis, Thalictrum, Anemone, Hepatica, Adonis and Actaea) and are visited by pollen-devouring or pollen-collecting insects.

These dissimilar structures, arisen from different floral organs, have to fulfil the same function of nectar presentation.  Some investigators (Prantl, 1888; Troll, 1928, p. 94) called these structures "honey-leaves" (meliphylls), or "nectar-leaves" (more recent term), which are more functional terms than morphological concepts (compare the terms: sporophylls, semaphylls, meliphylls in the section "Definitions and Terminology").

In a general way, differentiation of nectaries goes hand in hand with floral evolution, both processes controlled by the trophoclectic activity of progressively evolving contemporary pollinators.  Every level in floral evolution is consequently characterized by a certain stage of differentiation of the nectar-presentation mechanism, all coordinated with the successive development of the pollinators of these flowers (Fig. 11). Nigella is an exception (Brand, 1894-1895). In this genus the pleomorphic flowers are accompanied by extremely complicated nectar devices, with a special mechanism for closing and opening, and provided by perfect nectar guides.   The Nigella type was described first by Sprengel (1793) as one of his most significant discoveries.  In other genera such advanced nectar-presentation devices are associated with zygomorphic floral structures.

It is remarkable that the nectar-leaves described above occur only in the Ranunculaceae, where they appear first in the pleomorphic level and continue their differentiation in stereomorphic level.  All known nectar-presentation devices of other angiosperms are, according to Brown (1938) and Fahn (1953), considerably different in their structure and of different origin.  This indicates that concealed nectaries have arisen simultaneously in many higher angiosperms at a younger geological time (probably in the Tertiary period), when some groups of pollinating insects had reached a corresponding level in their sensory development, being able to locate and exploit hidden deposits of food.

## Secretion of Unconcealed Nectar

In lower evolutionary levels, the haplomorphic and actinomorphic flower types do not possess any protected nectaries.  In these flowers, the easily accessible sugary fluid, if any, attracts all kinds of visitors interested in sweetenings regardless of whether or not they act as pollinators.  These visitors creep in various ways and behave differently, frequently accomplishing only self-fertilization or leaving the flower

unfertilized.  These unskilled visitors do not look for the same flower
type they left, but tend to sit on any flower they see first.  Such pollina-
tors are wasting precious genetic material, often carrying their pollen
loads to wrong places.  Under these circumstances, unskilled insects
can have only slight significance as selective agents in floral evolution,
and such flowers tend to remain long unchanged.  Their main effort is to
attract as many visitors as possible advertising themselves by simple
colors or large size, by assembling small flowers into inflorescences
(many Umbelliflorae and Compositae), or by imprisoning their visitors
inside flowers.

## Formation of Concealed Nectaries

Apparently, such an insecure situation in pollination could not last
very long in such a phylogenetically progressive family as the Ranuncu-
laceae and specialization of nectaries became indispensable for the
further evolution of this family in the next pleomorphic level.  Actually,
the formation and differentiation of protected nectaries simultaneously
in several phylogenetic groups is a most natural phase of floral evolu-
tion that has its elementary beginning and all intermediate steps in the
Ranunculaceae.  Analogous trends in the evolution of nectaries are de-
scribed by Brown (1938) in many other angiospermous families.
    Comparison of the structure and development of nectaries in the
Ranunculaceae shows a gradual transition from the open nectaries to
simple nectar-pits and -cups, and from these to the complex nectar
presentation apparatus in higher levels (Fig. 11).  Simple nectar-pits at
the base of each petal of Ranunculus sceleratus L. and R. auricomus L.
are converted to protected cups in R. glacialis L. (Fig. 11:4-7).  In
Isopyrum and Helleborus the expanded limb of nectariferous petal has
completely disappeared so that an ordinary nectar-cup is formed from
the petal (Fig. 11:8-10).  In Trollius the nectariferous petal is much
reduced forming an elongated nectar-groove above its base (Fig. 9:3).  A
further progressive step in the evolution of nectar-leaves is observable
in the genera Delphinium and Aquilegia (Fig. 11:12, 13).  Here the nectar-
leaves are converted to long spurs, provided with round and curved tips,
the actual nectar depositories.  Spurs not only serve to secrete and con-
ceal nectar, but also attract visitors, being therefore brightly colored.
    In the highest evolutionary level of zygomorphic flowers of Aconitum
nectaries are completely concealed in remotest parts of the flowers
(Fig. 11:14-18).  However, the most remarkable nectary of Nigella (Fig.
11:11) is not connected by any intermediate link with other evolutionary
trends.
    Primitive pits and cups at the base of each petal of Paeonia, Pulsa-
tilla, Caltha, Ranunculus, Batrachium, and others are of such elemen-
tary structure that they could be easily formed on any floral organ al-
ready possessing nectar glands.  But even in these primitive pits and
cups, the more concentrated nectar is satisfactorily protected against
rain and evaporation, thus providing food of better quality to skilled
visitors able to locate these food deposits inside of flowers.  Such dis-
tinstive ability to remember and recognize nectariferous plants accord-
int to some floral characteristics is actually attributed to hymenopterous

and lepidopterous pollinators, which are the main visitors of the higher Ranunculaceae in the pleomorphic level and above. Concealed nectaries first appeared on the pleomorphic evolutionary level, where the archaic actinomorphic and haplomorphic types split, forming new distinguishable combinations of form and summetry. Reduction of multipetaloid actinomorphic corollas to definite numerical patterns must have occurred contemporaneously with differentiation of nectar-leaves in these flowers, thus providing certain types of nectaries marked by definite numerical patterns. Examples of such differentiation of nectar-leaves in correlation with floral specialization are numerous among the Ranunculaceae and other angiosperms.

Ample evidence is thus at hand that concealment of nectaries in the Ranunculaceae occurred first in the pleomorphic evolutionary level in close correlation with sensory development of their special visitors. These visitors progressively conditioned themselves to recognize and remember numeral patterns in association with hidden nectar deposits in flowers. Pentamerism, thereafter, became a symbol of deeply situated but rich nectaries in Ranunculus, Batrachium, Helleborus, Myosurus, Nigella, and other genera; it became a favorite pattern for nectar loving Apidae. Pentamerous flowers are predominant among present-day Ranunculaceae, occurring not only among pleomorphic flowers, but also in the stereomorphic and zygomorphic levels, as in Aquilegia, Delphinium and Aconitum, all well-defined bumblebee flowers.

However, pentamerism is not always associated with the presence of nectar in flowers of the Ranunculaceae. Anemone ranunculoides L., for instance, with five yellow petals, resembles the pentamerous, nectariferous flowers of the genus Ranunculus, but has no nectar. It is pollinated by pollen-collecting insects, and visited also by Apidae, which are vainly seeking nectar in these flowers (Knuth, 1908, p.12), thus completing pollination without reward.

It is reasonable to assume that the above-described phylogenetic partition of earlier ranalian groups must have produced various combinations of numeral patterns, some with nectaries and some without, but all exposed to the selective activity of their contemporary pollinators. Such is the common evolutionary trend among various species and genera of the present-day Ranunculaceae in the pleomorphic level. Anemone, Ranunculus, Caltha, Trollius, and other genera contain species with constant numbers (5, 6, 8) of petals and sepals (semaphylls), along with forms having an indefinite number of floral parts (Gertz, 1913; Losh, 1916; Rauh and Reznik, 1951). In some species, such as Hepatica triloba Chaix., similar variation occurs in the subspecific level (Plate 13; Table 3).

Similar variation also occurs in the structure and exposition of nectaries and nectar-leaves. In the genus Anemone, for instance, a variety of numerical patterns and colors exist without nectar and nectar-leaves. In Ranunculus, on the contrary, numerical patterns always are associated with certain types of nectaries. Yet, every one of these combinations is clearly innately conditioned to these iconic numerals; i.e. the combination of basic numerals, colors, size, and frequently also odors in these flowers.
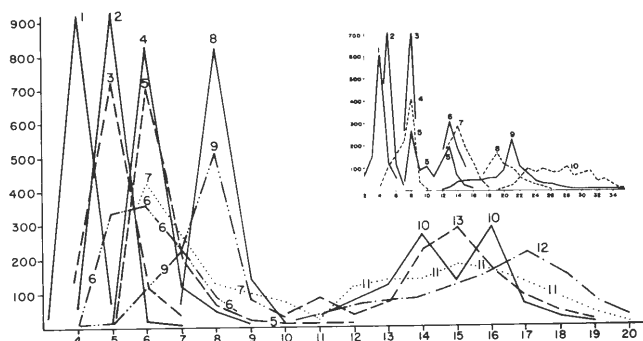
Figure 12. Variation in the number of petals (abscissa) of the flowers in the Ranunculaceae. Analyzed are 1000 flowers (in ordinate) from every species. Note that the pleomorphic flowers (1-9) have constant number of petals (or petaloid sepals) showing high, sharp peaks. Actinomorphic flowers (11-13), on the contrary, have indefinite number of petals and low peaks. Pictured are the following species: 1. Clematis verticillaris DC.; 2. Anemone canadensis L.; 3. Isopyrum biternatum (Raf.) T. and G.; 4. Eranthis hiemalis (L.) Salisb.; 5. Hepatica americana B.& B. Rydb.; 6. Anemonella thalictroides (L.) Spach.; 7. Ranunculus bulbosus L.; 8. Anemone japonica S.; 9. Ficaria verna Huds.; 10. Anemone apennina L.; 11. Adonis vernalis L.; 12. Anemone caroliniana Walt.; 13. Anemone decapetala L. Numerical data may be seen in Tables 1 and 2, explanation in text. A reduced scheme upper right is a similar grouping of the flower heads of the Compositae for comparison (after Leppik, 1960a, p.171).

### Conditioning of Insect-Visitors to Concealed Nectaries

Available evidence indicates that, parallel to floral evolution, considerable progression and specialization of pollinating insects must have occurred during the development of concealed nectaries in the Ranunculaceae. From the miscellaneous visitors of haplomorphic and actinomorphic types more skilled insect groups gradually arose with longer proboscides and more acute senses. These insects, being incessantly in search of better nectar sources, must have noted more rewarding concealed nectaries and must have memorized distinctive characteristics of these flowers. In addition to their well-established senses for color, odor, taste, form, and symmetry, a special sense for iconic numerals must have developed in visitors of pleomorphic flowers with concealed nectaries. Bees, bumblebees, moths, butterflies, and some droneflies are known to possess such sensory abilities and long enough proboscides to reach the concealed nectar.

## CLASSIFICATION OF FLOWER TYPES IN THE
## RANUNCULACEAE (Figs. 1, 13)

In view of the foregoing facts and findings, it is now possible to arrange all existing flower types of the Ranunculaceae into a system of six typologically graded series or "type-classes,"[10] as follows: amorphic → haplomorphic→ actinomorphic→ pleomorphic→ stereomorphic→zygomorphic (Fig.1). This series of successive typological stages appears natural and corresponds with the main evolutionary sequence of flower types, as described elsewhere (Leppik, 1957b, p.470, Fig.2). The sequence obviously conforms to the main trend of sensory development of pollinating insects.

An earlier system for typological classification of flowers was derived from a comparative hologenetic study of existing flower types in various geographic areas in the Old and New Worlds (Leppik, 1948a,b; 1949a,b; 1951a; 1952). Much stimulation for this work was obtained from a pamphlet by F. Merkenschlager (1940) about the "primitive" and "progressive" flower types and from his personal ideas and concepts about "Altstilen" and "Neustilen" in flowers. After some modifications in earlier orders and several terminological improvements the present system of "type-classes" (Leppik, 1957a) in flowers was completed during an additional study of tropical flower types in Central America (Leppik, 1953b; 1954a; 1955a,b,c,d; 1956a,b; 1957a,b,c). Later on this system was used as a yardstick for the determination of the relative sensory capabilities of anthophilous insects and birds to distinguish and remember certain flower types. Exact tests were performed with honeybees, bumblebees, wild bees, and tropical butterflies in Europe, in the United States, and in Central America. Results of this extensive study are but partly reported in various previous papers (Leppik, 1954a;1955b, c; 1956a,b; 1958; 1960a,b; 1963b).

### I. Amorphic type-Class

The most primitive amorphic type is not now known to exist among living Ranunculaceae. This elementary type-class very likely became extinct along with the early ancestors of this family. But it is not difficult to reconstruct a hypothetical amorphic flower for the ancestral Ranunculaceae, as proposed in a previous report (Leppik, 1948a). Such primitive flowers must have had distinctive semaphylls (undifferentiated perianth), probably arranged around many sporophylls without special symmetry, but distinctive from the vegetative leaves $(P_\infty A_\infty G_\infty)$.

### II. Haplomorphic Type-Class

Haplomorphic flower types in the Ranunculaceae are characterized by many distinctly colored large semaphylls, frequently arranged in a semispheric pattern, as in Magnolia, Nymphaea, Nelumbo, Calycanthus, Paeonia (Fig. 9), and other primitive genera of the order Ranales. Showy parts (semaphylls) of these flowers are formed from morphological petals, petaloid sepals, bract, or modified staminodes. Colors are simple, frequently greenish, white, yellow, seldom pink or red, always
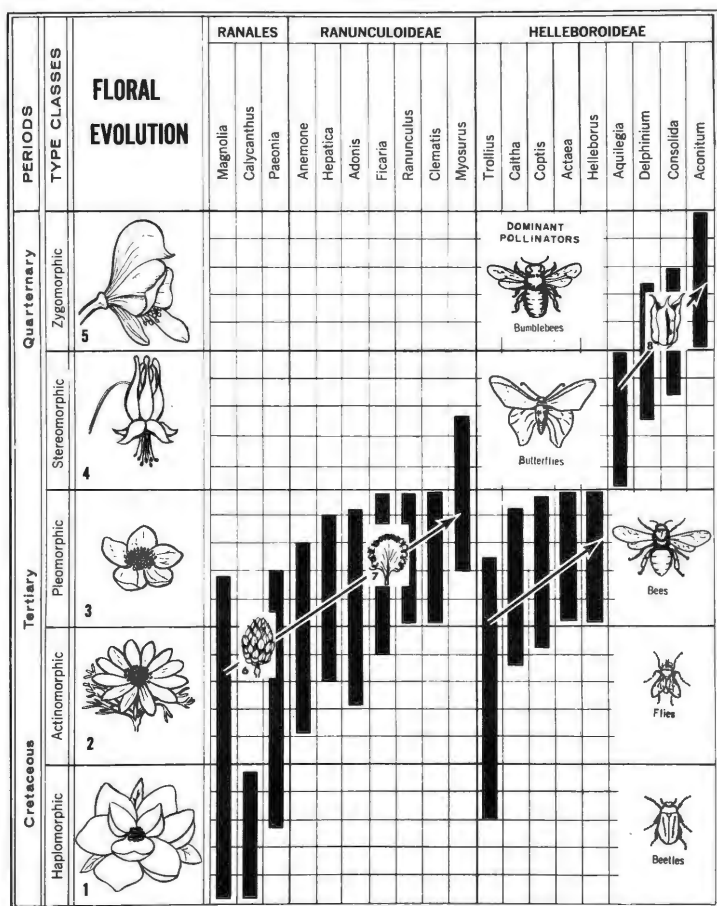
Figure 13. Floral evolution in the Ranunculaceae. Flower types (1-5) in left column indicate the evolution of type-classes in historical sequence (haplomorphic through zygomorphic). Black columns in the middle show the actual coverage of corresponding type-classes of genera. Arrows point to the phylogenetic trends in the development of fruits (6-8). Dominant pollinators of every type class are pictured right. Numbers indicate: 1. Magnolia; 2. Adonis; 3. Ranunculus; 4. Aquilegia; 5. Aconitum. Fruits: 6. Magnolia; 7. Ranunculus; 8. Aconitum.

distinctive from green leaves and yellow stamens, but never variegated in the same flower.

Such large flowers are readily distinguished by pollinators from a considerable distance and seldom are compiled into loose inflorescences. They are accessible to practically all pollinators, but in recent floras are visited mainly by beetles, flies, and other insects whose instincts and sensory abilities do not reach higher than the corresponding simple stage of their sensory development. It is not difficult to guess that the visitors of haplomorphic flowers do not require the ability to distinguish radiate symmetry, numerical patterns, variegated colors, nectar guides, and many other special structures of the higher type-classes.

Truly haplomorphic flower types are not found very frequently among the Ranunculaceae. Best represented is the primitive genus Paeonia, but even in this genus there are marked trends toward actinomorphic and pleomorphic type-classes. The haplomorphic shape of flowers of Trollius is apparently a regressive trend in this otherwise advanced genus. (Fig. 9.)

Ranunculus lyallii Hook f. which occurs in the high mountains of New Zealand has very large magnoloid flowers, up to 5 inches in diameter consisting of 40 to 60 white petals (nectar-leaves). This is a shrubby plant with primitive characteristics, possibly a relict from the earlier haplomorphic representatives of the Ranunculaceae. Another example is the genus Laccopetalum from Peru, described by Ulbrich (1906).

Among related families, a well-differentiated haplomorphic flower type in the genus Magnolia can be traced back according to fossil records to the early Cretaceous period, roughly estimated 100 million years ago (Leppik, 1963a, b).


### III. Actinomorphic Type-Class

Actinomorphic floral patterns can be derived from Haplomorphic types by flattening the sporophylls, semaphylls, and nectaries into the same level. The effect of such radiate flowers is still heightened by long and narrow petals and by color contrast between peripheral (white petals) and central parts (yellow stamens) of the flowers.

This type, which had its early beginning in the archaic Cycadophyta, was common among mesozoic Bennettitales (Leppik, 1960, 1963a, b). Its floral pattern resembles the radiate symmetry of cycad leaves and very likely has been deeply engraved into the innate memory of early pollen-eating insects. These insects, predominantly beetles, presumably had to distinguish their food plants according to cycadeoid leaf pattern from less nutritive ferns and horsetails. It is no wonder, therefore, that the radiate floral pattern became common not only among the Bennettitales, but also in numerous cantharophilous angiosperms, as soon as these appeared on the scene.

Actinomorphic flower types occur occasionally among Ranunculaceae. Anemone apennina L. (Plate 6), A. caroliniana Walt., A. blanda Sch. & Ky. (Plate 5), Adonis, Helleborus, and others have distinctly actinomorphic flowers.

## IV. Pleomorphic Type-Class

Pleomorphic flowers can be derived from actinomorphic types by re-
ducing the polypetalous corolla to a certain numerical pattern, such as
8, 6, 5, 4, and 3 or by alternating petals with sepals: 6+6, 5+5, 4+4,
and 3+3. To distinguish such numerical patterns in flowers is beyond
the ability of beetles, but the system can be well mastered by several
groups of hymenopterous and lepidopterous pollinators (Leppik, 1953c,
1957c). Obviously, insects cannot distinguish numbers in flowers by
counting or computing in the anthropomorphic sense of these words, but
they can recognize at sight the octo-, hexa-, penta-, tetra-, tri-, and
polymerous flowers as definite symmetrical patterns (Leppik, 1953b;
1954a; 1955a, b, c; 1956a, b; 1958).
     Pleomorphic flowers are very common among the Ranunculaceae.
Octomerous (Anemone japonica, Plate 9, above), hexamerous, tetram-
erous, and most frequently pentamerous flowers occur sometimes in the
same genera, as in Anemone, Ranunculus, Helleborus, and others (Plate
10, 11, 12, 13, 14).

## V. Stereomorphic Type-Class

Stereomorphic flowers with protected nectar deposits are stretched
toward a third dimension. Some pleomorphic (frequently pentamerous)
pattern is displayed in the front of the flower; but stamens, pistil, and
particularly nectar are hidden. Such structures require of the pollina-
tors a particular ability to distinguish three-dimensional patterns in
order to locate the hidden nectar in the depth of  he flower and a long
enough proboscis to reach it.
     That the stereomorphic types actually are evolved from pleomorphic
patterns is convincingly demonstrated in the floral differentiation of the
Ranunculaceae, with all intermediate stages between these two types. In
the genus Aquilegia, for instance, some primitive Asiatic species, such
as A. ecalcarata Maxim., still bear regular pentamerous corolla without
spurs or other signs of stereomorphism. Most advanced species, on the
contrary, can easily be arranged in a progressive sequence according to
the development of spurs (Plate 15, 16). A remarkably elementary type
of stereomorphism is represented in the slightly spurred pentamerous
flowers of Myosurus.
     Stereomorphic types are common among tubulate flowers whose cor-
ollas are stretched into long nectar-holding channels. Yet, the flowers
of the Ranunculaceae are choripetalous in their morphological structure,
without storage space for nectar in corollas. It became necessary,
therefore, for the stereomorphic genera Aquilegia and Delphinium to
form special tubular or saclike projections or "spurs" on petals for ac-
cumulation of nectar (Plate 15, 16). The spur develops secondarily here
as a down-growth of the central part of a petal primordium which was
originally flat (Tepfer, 1953, p. 551). Thus, stereomorphic flowers have
evolved parallel in many phylogenetically distinct plant groups in an
adaptive response to the selective activity of pollinating insects. Such
floral structures could not evolve before the pollinators reached the
corresponding ability to orient in the three-dimensional space, starting
thereafter to select flowers with longer tubes and deeper nectar deposits.

Among the Ranunculaceae, the genera Myosurus, Aquilegia, and Delphinium have stereomorphic flowers. Aquilegia is unique for its five spurs (Plate 16), one in every petal, thus resembling a compound flower. Delphinium (Plate 15) has a single spur in each flower, but shows a slight bilateralism in its corolla, thus being an intermediate stage between stereomorphic and zygomorphic type-classes. Similar spurs which have evolved from sepals in Tropaeolum (Tropaeolaceae), Impatiens (Balsaminaceae) and Melianthus (Melianthaceae) and are described by Werth (1941).

## VI. Zygomorphic Type-Class

Zygomorphic floral structures belong to the most complicated pollination systems, which require the highest sensory ability of pollinators. In these structures, all previous developments and achievements, such as pleomorphism, stereomorphism, bilateral symmetry, and, not least, variegated colors and fine odors, are harmoniously combined in the same flower. Numerical patterns, however, are fully preserved but exquisitely streamlined into personate, labiate, papilionaceous, or other three-dimensional corollas, in which the iconic numerals have lost their true meaning and visual effect. For instance, it can be seen that the gamopetalous corolla, of the Scrophylariaceae, Labiatae, Papilionaceae, and many other zygomorphic flowers are actually formed from five coalescent petals, but the number five has practically disappeared from the floral picture and does not help to distinguish this flower from trimerous or tetramerous corollas.

In addition to all these characteristics, a high degree of specialization is introduced in the zygomorphic flower types, which makes them accessible only to very restricted groups of pollinators, capable of locating and reaching the hidden nectar deposits in these flowers. Consequently, the great mass of less capable insects are excluded from the process of fertilization, and only the most specialized pollinators have access to zygomorphic flowers.

Among the Ranunculaceae, only the genus Aconitum has truly zygomorphic flowers. The morphological structure of these flowers is unique and highly specialized, revealing the long evolutionary history of this genus. (Plate 18.)

Numerous stamens and polymerous perianth of Aconitum (Fig.13:5) clearly indicate an early haplomorphic structure, from which the present flower must have evolved through actinomorphic, pleomorphic, and stereomorphic stages. Eight reduced petals are the obvious remains from a previous actinomorphic corolla, which has lost its sematactic function in the present order. Five sepals point to a previous pentamerism, which later became replaced by zygomorphic structure. In accord with the present floral system, petals have lost their original function as semaphylls and have degenerated, except two, which developed elongated spurs with nectar glands in the coiled tops. In this new arrangement, sepals took over the ecological function of degenerated petals by resembling colored pentamerous corolla, as in most members of the subfamily Helleboroideae. Thus, the final step in floral evolution of Aconitum is zygomorphic, which completely changed the floral picture.

The genus <u>Aconitum</u> is a typical bombophilous planf, or "bumblebee-flower par excellence"—as Kronfeld (1890) expresses it (Fig. 14). The size, colors, symmetry, suppressed numerical patterns, and pollination mechanism of monkshood correspond to the special sensory traits and physical abilities of bumblebees. Large sepals of the monkshood are blue, violet, yellow, or hrightly mottled, and in conjunction with the smaller petals, serve as semaphylls to attract pollinators. These colors are considered to be attractive to hymenopterous pollinators, particularly to bumblebees. Conspicuousness of single flowers is markedly increased by the aggregation of the flowers into racemes, which bear numerous blossoms.



Figure 14. World distribution of bumblebees (solid line) and the genus <u>Aconitum</u> (dotted line) according to Kronfeld (1890).

The two upper petals are converted into long-stalked hoodshaped nectaries, varying in size and structure in different species (see Fig. 11: 14-18). The simplest form occurs in <u>Aconitum heterophyllum</u> Wall., native to East India, with a thick stalk, expanding into a cap open below with no spur. This species is considered by Rapaics (1907, 1908) to be one of the oldest relicts of central Asia where the presumably original area for the monkshood lies. In <u>A. palmatum</u> Wall. the spur makes its first appearance as a slight projection (Fig. 11:14). Further evolution of spur is marked by <u>A. napellus</u> L., with a somewhat larger spur (Fig. 11: 15), <u>A. anthora</u> L. (Fig. 11:16), <u>A. septentrionale</u> Kolle, with spur rolled inwards (Fig. 11:17), and <u>A. lycoctonum</u> L. with extended stalk about 20 mm long and inward rolled spur coiled into a spiral of $1\frac{1}{2}$ turns (Fig. 11:18).

Further evolutionary correlation between monkshoods and bumblebees is seen in the size of both partners. The body of a bumblebee exactly fills the interior of the floral parlor, so when Kronfeld (1890) made a plaster cast of a monkshood flower, it corresponded in a remarkable way to the shape of a medium-sized female bumblebee.

Since the seed production of the monkshood depends on pollination by bumblebees, this plant must become extinct in places where bumblebee visits fail. Therefore the area of distribution of the genus Aconitum is entirely included in that of the genus Bombus (Fig. 14).

It is no wonder, therefore, that the more primitive flower types on the haplomorphic and actinomorphic levels show all characteristics of cantharophily and myophily, whereas the upper levels become progressively melittophilous. Such evolutionary sequence concurs adequately with the relative ability range of various groups of pollinating insects to distinguish flower types, as pictured in a previous report (Leppik, 1957b, p.473, Fig.3). It also corresponds to the presumable sensory evolution of anthophilous insects.

## WINGED VISITORS OF THE RANUNCULACEAE
(Fig.15, Table 5)

The visitors and pollinators of the Ranunculaceae belong to all insect orders, but not all ranalian flowers are readily accessible to all these insects. Specialization of visitors to certain flower mechanisms has evolved hand in hand with the differentiation of flower types in a well-established sequence from the haplomorphic level up to the zygomorphic stage, as pictured in Figs. 1, 15.

Haplomorphic and actinomorphic flowers are accessible to all insects but are visited mainly by beetles, flies, ants, and other unskilled pollinators. These insects are satisfied by pollen, low-grade nectar secreted openly inside the flowers, or edible flower parts. Ants, for instance, lick the sugary juices on flower buds of Paeonia. These ants do not carry pollen, but their activity and secretion is believed to stimulate flower buds to open.

Higher pollinators, such as butterflies, bees, and bumblebees seldom visit haplomorphic flowers except when these insects require pollen, or are short of food from higher types. Apidae are specialized to higher floral mechanicms and remain steadfast to zygomorphic, stereomorphic or pleomorphic types, as long as they still can find food in these flowers. Müller (1883) established the continuous gradations from the insect groups that never visit flowers to those which seek secondary food from blossoms and finally to those which depend entirely on nectar. He believed that these insects whose early ancestors did not visit flowers, gradually become habituated to a floral diet, correspondingly modifying their mouth parts and "learning" to operate more and more complicated pollination mechanisms. Delpino's (1868-1874) teleological conception that certain flowers have been predestined for certain insects and vice versa, consequently, is untenable.

### Coleoptera

Beetles are the most numerous but least skilled pollinators of the Ranunculaceae. Their sensory abilities do not enable them to exploit hidden nectaries in higher flower types, which they occasionally visit. Sometimes beetles even do great damage to their food plants by nibbling

ovaries and other flower parts. Nevertheless, beetles'were greatly involved in the evolution of haplomorphic and actinomorphic types, and remain even now the main pollinators of these classes (Fig. 15).

The main characteristics of beetle-pollinated flowers (or inflorescenses) are large haplomorphic or actinomorphic shape; open nectaries, if any; simple colors such as white, yellow, greenish, or pinkish; frequently strong odors. There are no nectar-guides, no depth effects, and no tendencies to bilateralism or zygomorphism in beetle-pollinated flowers.

In spite of these clear distinctions, already well established since Delpino (1868-1874), there has been a long dispute among anthoecologists about the true status of cantharophilous flowers. For instance, Jaeger's (1957, p. 394) viewpoint that there is no cantharophily at all is opposed by Pijl (1961, p.44) in the statement that "the flower is fundamentally a beetle-flower and many have remained so or have become so." Obviously, both these authors are right, approaching the subject with different viewpoints. There are no specialized beetle-pollinated flowers, because these elementary types are accessible to and adapted for all pollinators, skilled or unskilled. But, historically, beetles very likely were so numerous and have been so fundamentally involved in the evolution of primitive flowers that the main characteristics of these elementary types might be considered to be cantharophilous. Actually, from these general structures, all specialized types can be derived successively, as pictured in Fig. 1. Beetle pollination is frequently discussed by classic and modern florecologists including Delpino (1868-1874), Müller (1883), Diels (1916), Pijl (1960-1961), and others.

In addition to beetles, there were undoubtedly numerous other insects at work. Many recent representatives of old insect groups, such as Hemiptera, Neuroptera, Orthoptera, and Diptera, feeding on pollen, nectar, or soft flower parts, frequently act as pollen carriers. But these insects are actually on the same, or an even lower level, with beetles and, therefore, must have reacted to the flowers in a way similar to beetles. Their selective activity among flowers, if any, could not have been very significant. In a general way, the sensory development of anthophilous insects must have been much the same in its lower levels, having become more and more specialized in the upper stages.

## Hymenoptera

Among hymenopterous pollinators, bees and bumblebees (Apidae) are undoubtedly the most skilled and capable visitors of the Ranunculaceae. These insects obviously have played the chief part in the evolution of flowers above the actinomorphic level. Very likely they were the first insect pollinators that developed the ability to distinguish numerical patterns in flowers, thus causing, by their selective activity, differentiation of iconic numerals in pleomorphic and stereomorphic levels. In still higher levels, the selective activity of bumblebees became so effective that a new zygomorphic trend evolved out of stereomorphic flowers.

Bees and bumblebees are the best known plant pollinators, extensively studied by Müller (1883), Kronfeld (1890), Knuth (1908), Frisch (1914-1954), Lovell (1918), Werth (1941), Kugler (1943-1955), Grant (1949-1952),

Ribbands (1953), Vogel (1954), Kerr (1956), Nogueira-Neto (1948-1953),
Jaeger (1957), Lindauer and Kerr (1958), Pijl (1960-1961), Lindauer
(1961), Löken (1961 and other papers), Sprague (1962), Percival (1962),
Faegri (1963), and many others.

## Lepidoptera

Butterflies and moths, in their perfect state, restrict themselves al-
most entirely to nectar as their food. This adaptation has reduced their
mouth-organs into a long, thin suctorial tube that can be inserted into
deep nectaries. No wonder, therefore, that their special flowers have
long tubes or spurs, inaccessible to short-tongued insects. In the Ran-
unculaceae, Lepidoptera, particularly the Sphingidae, can be observed
most commonly sucking nectar from the long-spurred Aquilegia and
Delphinium and occasionally from other genera. Yet, the evolutionary
significance of Lepidoptera cannot be compared with that of beetles, bees
or bumblebees.

## Flower Visitors Observed on the Ranunculaceae

Extensive statistical data concerning the flower visitors of the Ranun-
culaceae are furnished by many classic and modern anthoecologists,
such as Delpino (1868-1875), Müller (1883), Kronfeld (1890), Ekstam
(1895), Knuth (1908), Robertson (1928), Leppik (1948a, 1958), Löken
(1961), and others. Unfortunately, this material is not uniform, con-
taining mostly European or North American species, without much infor-
mation about Asiatic, African and other tropical representatives of the
family.

In spite of this and other shortcomings of these data, they neverthe-
less unanimously confirm the above proposed theory of the mutual inter-
relationship between insects and flowers as reciprocal selective factors
in evolution. The sequence of floral evolution from the haplomorphic and
actinomorphic type-classes up to the zygomorphic level is also most
convincingly demonstrated in the ability grades of insects to exploit the
floral resources at different evolutionary levels.

Table 5 summarizes all available data from the literature, including
personal observations of the writer, arranged according to the above-
described sequence of corresponding types. These data are pictured
graphically in Fig. 15. Excluded from this list are occasional sojourners
of flowers not involved in the process of pollination. Ants, for example,
frequently crawl into open flowers and lick the sugary fluids of plants
without carrying pollen from flower to flower. Beetles and flies are
effective pollinators of haplomorphic and radiate flower types and are
frequently found sheltering also in Aconitum flowers. But in the latter
they are able neither to locate the nectar nor to act as pollinators.

The frequency of insect-visitors, registered by the above-mentioned
investigators, on the present-day Ranunculaceae, is pictured in Fig. 15.
Black columns indicate the approximate number of observed visitors in
each type-class (II-VI), paralleled with the historical sequence of floral
evolution at the left.

It appears from this sketch that the main builders of flower types in

Table 5. Total number of visitors of the Ranunculaceae combined from all known sources and arranged according to historical sequence of type classes. See Fig. 15.

| Type classes and Plants | Orthop-tera | Neurop-tera | Coleop-tera | Diptera | Hemip-tera | Thysa-noptera | Lepi-doptera | Hymenoptera bees | bumbleb. | Birds |
|---|---|---|---|---|---|---|---|---|---|---|
| **VI. Zygomorphic:** | | | | | | | | | | |
| Aconitum div. spp. | | | | | | | | | 634 | |
| **V. Stereomorphic:** | | | | | | | | | | |
| Aquilegia div. spp. | | | | | | | 6 | 72 | | 1 |
| Delphinium div. spp. | | | | | | | 8 | 23 | 29 | 1 |
| Consolida arv. | | | | | | | | | 10 | |
| Nigella div. spp. | | | | | | | | 8 | 5 | |
| **IV. Pleomorphic:** | | | | | | | | | | |
| Ranunculus div. spp. | | | 272 | 2226 | 163 | | 738 | 2626 | 23 | |
| Ficaria verna | | | 7 | 24 | 145 | | 23 | 435 | 37 | |
| Pulsatilla div. spp. | | | 34 | 16 | 34 | 17 | 5 | 14 | 34 | |
| **III. Actinomorphic:** | | | | | | | | | | |
| Anemone div. spp. | 6 | 2 | 5 | 45 | 4 | 73 | 5 | 70 | 20 | |
| Adonis div. spp. | | | 7 | 5 | 6 | 15 | 5 | 18 | 46 | |
| Hepatica spp. | | | 2 | 17 | | | | 27 | 7 | |
| **II. Haplomorphic:** | | | | | | | | | | |
| Paeonia spp. | 4 | 7 | 361 | 217 | 16 | 27 | | 4 | 3 | |
| Magnolia | | | 17 | 5 | 3 | | | | | |
| Nymphaea | | | 36 | 7 | | | | 1 | 1 | |
| Victoria regia | | | 10 | | | | | | | |
| Nuphar luteum | | 1 | 3 | 3 | | | | | | |
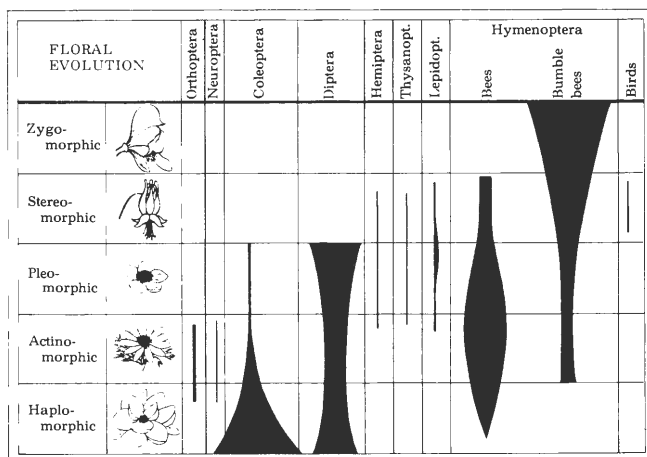
Figure 15.   Frequency of insect-visitors registered on corresponding
        type-classes of the Ranunculaceae.   Black columns indicate total
        number of visitors observed on the flowers of corresponding type-
        classes (see Table 5, explanation in text).   Note the dominance of the
        Coleoptera,  Diptera,  and  Hymenoptera  in  the  pollination  of  the
        Ranunculaceae.


It appears from this sketch that the main builders of flower types in
the present-day Ranunculaceae have very likely always been Coleoptera,
Diptera, and Hymenoptera.
    All other insects and birds are represented in such small number that
their selective influence in floral evolution cannot be very significant.
Exceptions are a few sphingophilous and ornithophihous types of Aquilegia
in the stereomorphic level.   Paleontological evidence indicates that both
butterflies and birds are latecomers among plant pollinators, at a time
when the floral evolution had reached the pleomorphic level.


                    BIOCHEMICAL EVOLUTION IN THE RANUNCULACEAE

    There is little or no doubt that the selective activity of pollinators,
causing a far-reaching morphological differentiation in flowers, must
also produce a considerable biochemical change in plants exposed to this
selection. More concentrated nectar, attractive colors, and intense odors
in higher evolutionary levels indicate a progressive change in the meta-
bolism of evolving plants.

But, unfortunately, no research results are yet available to correlate morphological differentiation with biochemical evolution in plants. Some preliminary investigations of Ullrich (1932), McNair (1934, 1935), and Gibbs (1945) show that some chemical and physical properties of fats, volatile oils, and alkaloids vary in accordance with the degree of evolution of the plant families containing them.     McNair found that generally, the more highly organized the plant, the more complex are its chemical products and vice versa. Some general problems about color evolution in flowers are discussed by Weevers (1952), but no special research has yet been done on the Ranunculaceae.

## GENERAL RETROSPECT

The almost complete absence of early paleontological records in this predominantly herbaceous family is at least partly compensated for by a well-preserved sequence of primitive morphological characteristics, preserved at the genus and species levels in the Ranunculaceae. There are genera and species with primitive characteristics still living side by side with more advanced or even highly specialized types, thus revealing an extensive evolutionary specialization throughout the family. In these circumstances, it is not difficult to restore the complete evolutionary sequence of flower types in the Ranunculaceae.

### Primitive Flower Types in the Ranunculaceae

It is obvious now that the most elementary floral form among living Ranunculaceae is the haplomorphic magnolioid type, as represented in the most primitive section Moutan of the genus Paeonia. Its main characteristics are the spiral arrangement of numerous floral parts around a central axis, which progressively tend to become cyclic in the higher evolutionary levels. Yet, this type class is also common among early angiosperms, such as the Magnoliaceae, Illiciaceae, Calycanthaceae, Nympheaceae, and other primitive flowering plants. Being associated with beetles and other primitive pollinators, this type-class can be traced back, according to fossil records, until the early Cretaceous period, roughly estimated 100 million years ago (Leppik, 1960b, 1963a, b).

Further paleontological records indicate that haplomorphic flowers, reflecting the corresponding sensory level of their contemporary pollinators, were common throughout the Cretaceous period and in the beginning of the Tertiary period (Leppik, 1963b). Since Tertiary, however, they were gradually suppressed by advancing pleomorphic and stereomorphic types; but, in spite of this competition they survived together with their primitive pollinators up to modern floras, where they still have a significant position. Similarly, beetles, flies, bugs, and other primitive pollinators, in spite of their restricted sensory abilities, survived all competitions with specialized insects and are still important pollinators of primitive flower types.

One can assume, therefore, that the ancestors of the present-day Ranunculaceae (tree peonies possibly among them) already occurred, along with other primitive angiosperms, in the northern hemisphere

during the Cretaceous period. Their flowers must have been originally of haplomorphic form, the commonest type in the Cretaceous period, and their pollinators very likely were beetles, flies, and wasps, whose fossils frequently are found in the same beds with early angiosperms.

Flowers of haplomorphic type are accessible to all pollinators capable of recognizing these flowers from a distance. Present-day peonies, for instance, offer food and shelter to numerous insects, both big and small, including beetles, flies, fleas, ants, wasps, honeybees, bumblebees, and tiny thrips.

Geographical distribution of the recent Ranunculaceae shows that the genera bearing haplomorphic and actinomorphic flower types have almost a cosmopolitan spread, including some remains from the old Gondwana flora in the southern hemisphere. In contrast the genera with stereomorphic and modern zygomorphic flowers, such as Aquilegia, Delphinium and Aconitum, live today exclusively in arctic and temperate floras of the northern hemisphere (Fig. 14). This fact indicates an evolutionary parallelism in the floral differentiation of the Ranunculaceae and the sensory development of Apideae, the main pollinators of stereomorphic and zygomorphic Ranunculaceae in the northern hemisphere. Obviously, the above-mentioned genera could also live in appropriate climatic conditions in the southern hemisphere as their actinomorphic relatives do, where they would have the special pollinators for their reproduction.

## Differentiation of Numerical Patterns in Correlation
## with Development of Concealed Nectaries

An important change in floral evolution was introduced on the pleomorphic level by reduction of polymerous flower types to some definite numerical pattern, such as three, four, five, six, and eight, as most common numbers in flowers. Contemporaneously with this outside change, various types of nectaries began to develop in flowers. In concealed nectaries, food of better quality was offered to more skilled pollinators capable of locating hidden nectaries and possessing a proboscis long enough to reach the nectar.

Obviously, this was an important turning point in floral differentiation that permitted mutual specialization between flowers and their pollinators and vice versa. From that point on, more progressive insect groups, including bees, butterflies, and some flies, concentrated more and more in their visits and selective activity upon their special food plants, thus becoming typophile (steadfast, "typenstett") to certain types during their successive flights. Thereafter, a rapid evolutionary expansion followed, not only in the Ranunculaceae, but also in other fast-progressing families of flowering plants. Fossil imprints indicate that pleomorphic flower types became dominant at the beginning of the Tertiary period, particularly during the expansion of herbaceous plants in grassland areas (Leppik, 1963b).

Ample evidence indicates that in the Ranunculaceae, nectaries arose independently in different phylogenetic groups and then underwent various modifications. This situation most convincingly demonstrates the close evolutionary relation between the differentiation of flower types and the sensory development of their pollinators, as described earlier.

It also confirms the antiquity and basic position of the Ranunculaceae among other angiosperms.

It is substantially certain now that the Ranunculaceae must have evolved at a time when some pollinating insects gradually began to change their feeding habit from pollen to concentrated nectar. There is some conclusive evidence that this change must have occurred in the end of the Cretaceous and the beginning of the Tertiary periods.

## Trophoclexis vs. Selection

Although little has been learned directly about the internal sensory reaction in insects to the flower types, such information has accumulated indirectly through experimental analyses and direct observations of flower-visiting insects. The actual selective activity of pollinators, conducted by their food searching (trophoclectic)[13] instincts, can now be better understood.

Müller (1883, p.593) assumed that "insects must operate by selection in the same way as do unscientific cultivators among men, who preserve the most pleasing or most useful specimens, and reject or neglect the others. In both cases, selection in course of time brings those varia-tions to perfection which correspond to the taste or needs of the selec-tive agent." This basically correct but physiologically oversimplified explanation did not satisfy later explorers, who set forth several anti-selectionistic theories (see Discussion). However, in the light of recent study, a far better explanation can be offered.

Contrary to Müller's assumption, a fundamental difference exists between the conscious plant selection conducted by man and the food-searching activity of insects. Man can see the fruits, berries, or other plant organs in which he is interested; he can make his conclusions im-mediately after tasting. Insects, on the contrary, seldom can see their food as yellow pollen or glistening nectar droplets in the primitive flower types at a close distance. In all these cases where nectar is invisible insects must make their choice from a distance, seeing the flower as a whole. Pollinators must know in advance which flower types contain nectar of higher concentration and which flowers are less rewarding. In this way insects can save much time and energy, which otherwise would be needed for examination of every single flower in a foraging area. In the long run even a very slight saving of time and energy becomes in the aggregate of great importance for the survival of the species as a whole. Flowers with concealed nectaries can be chosen only according to type or some special floral characteristics visible from a distance.

On the other hand, once a visitor has already landed on a flower he possibly may complete pollination even when he does not find any food. Many flowers, like Anemone ranunculoides in the preceding discussion, attract visitors by stimulating their instincts without offering any reward.

Accordingly, insects have to operate persistently with symbols, and rely on their instincts and senses in all these cases, while man uses his intelligence and makes his decision according to personal taste and

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[13] Trophoclexis is the food-searching activity of pollinators connected with selection of better food plants according to floral characteristics.

judgement. In the long run, this situation has caused anthophilous insects to develop their particular sensory system for floral characteristics. In an incessant search for better nectar plants, "they must prefer some flowers and reject or neglect others," as Müller puts it. This trophoclectic activity of insects is most convincingly demonstrated in the historical sequence of floral development in the Ranunculaceae, as pictured in Fig. 13.

### Evolutionary Correlation between Euanthial Flowers of the Ranunculaceae and Pseudanthial Flower Heads of the Compositae

Composed of numerous pentamerous florets (flosculi), a flower head (capitulum) of the Compositae as a whole resembles in its shape a single flowers, rather than an ordinary inflorescence. Still more striking is the fact that these "pseudo-flowers" ("pseudanthia" versus "euanthia" according to Troll, 1928) frequently imitate the "true flowers" in the phylogenetically remote family of the Ranunculaceae. This apparent paradox of evolutionary convergency has produced a good many theories and controversial explanations that are reviewed and criticized recently by Burtt (1961, 1962). An unexplained genetic mechanism in the Compositae tends to reduce the strictly pleomorphic pentamerous florets to a minimum size necessary for quick production of a maximum number of single-seeded fruits (achene). In addition to their minimum weight such tiny fruits are well equipped with feathery pappus for instant dispersal by wind. For this purpose the minute flower size has an obvious advantage and a selective value in an open landscape, the common habitat of the Compositae.

An opposite trend, however, which appears to be controlled by selective activity of pollinating insects, leads to the restoration of definite floral patterns necessary for attraction of pollinators. Thus a large number of tiny florets are gathered into a sizeable head to look like solitary flowers. In this new configuration ray florets simulate petals, and disc florets stamens, the sepals being replaced by the involucral bracts. Such "pseudo-flowers" imitate definite ranalian flower types in shape, size, color and number of flower parts and are actually distinguished as such by insect visitors. These opposite but reciprocally compensating evolutionary processes are repeated in genus after genus throughout the whole family of the Compositae, as shown in the enclosed plates.

Imitations of haplomorphic flower types are common among Dahlia, Sonchus, Taraxacum, Zinnia, and many other genera of the Compositae. In Plate 2 a white flower of Magnolia soulangiana Soul.-Bod. is compared with a capitulum of Tithonia speciosa Hook. Both are alike in size, shape, posture, and general proportions, representing the common haplomorphic type class. Plate 4 shows a single flower of Trollius chinensis Bunge, compared with the head of Calendula officinalis L.

Actinomorphic types, like sunflowers, daisies, marigolds, and asters are the dominant patterns among the flower heads of the Compositae. They imitate the radiate flowers of the Ranunculaceae, as compared in the enclosed tables. In plate 5 a single flower of Anemone blanda (Sch. Ky.) is compared with Gaillaridia grandiflora Hort. Both have similar radiate shape and color patterns. Anemone apennina L. has similar

radiate shape as Dimorphotheca aurantiaca DC. in Plate 6.   Pyrethrum roseum Lindl. and Chrysanthemum thunbergii Lindl. in Plate 7 are further examples of actinomorphic flower heads that resemble single flowers in the Ranunculaceae.   Helenium autumnale L. and Actinea odorata L. in Plate 8 have similar radiate shape but differ from one another in the number of ray florets.

Less frequent are the pleomorphic types.   In Plate 9 an octomerous capitulum of Cosmos bipinnata Cav. is compared with the flower of Anemone japonica S.  Both have similar pleomorphic shape, approximately the same size, and white or pink color.  Tagetes signatus Bartl. in Plate 11 is compared with Caltha  palustris  L. and micranthous Galinsoga ciliata (Raf.) Blake in Plate 12 with flowers of Ranunculus sceleratus L.

It appears from this comparison that the "pseudoflowers" in the Compositae have a more perfect shape and symmetry, with neatly emarginate rays (see Plates 8, 11, 12), than the more robust petals of the Ranunculaceae.   This all shows the more primitve position of  the Ranunculaceae and more progressive level of the Compositae among angiosperms.

Further evolutionary parallelism between  the flowers of the Ranunculaceae and the flower heads of the Compositae is expressed in the marked reduction of semaphylls in the pleomorphic level of both families. Statistical counts of the petals in the ranalian flowers and ray florets of the composites deliver a similar graph as pictured in Fig. 12.   In both cases the number of petals and rays were counted in 1000 flowers or flower heads of the same species, as shown in Tables 3 and 4.  Prevailing numbers are in both cases "eight" and "five" that show sharp peaks in Fig. 12. Depending on the level of sensory development of pollinators, progressive and regressive trends are observable: actinomorphic $\rightleftharpoons$ pleomorphic and vice versa.

### Typological Grouping and Taxonomic  Classification
### in the  Ranunculaceae

It appears from the foregoing discussion that the  above-described system of type-classes of flowers (see pp. 42-47 and Fig. 1, p. 7) do not match well with the phylogenetic order, and that the typological grouping of flowers differs essentially from the taxonomic classification of the Ranunculaceae.  This is because the taxonomic classification is founded on the phylogenetic relationship in plants, while the typological grouping of flowers is a floroecological system that is based on the sensory reaction and selective activity of plant pollinators.   Large insect groups, or different insects of the same stage of sensory development are working in various floras, selecting from phylogenetically different plants flowers with similar characteristics until they finally have reached the same types in different taxonomic units.   The cases of convergency, parallel development, and recapitulation of the same evolutionary sequence in different taxonomic plant groups are common throughout.   A parallel evolution is consequently going on simultaneously in many plant groups, which may or may not be related genetically.

Inside hereditary and genetic factors in plants are producing new gene combinations, new idiotypes, and mutants in flowers.   But it depends on

the sensory reaction of pollinators which new types they select as their
food plants for permanent visits.   In this way internal and external fac-
tors interact on the course of floral evolution, as described in several
previous papers (Leppik, 1957b, p.469; 1961a, p.23).

Floral evolution, therefore, depends on the interaction of internal
(phylogenetic) and external (hologenetic) factors that tend to convey the
course of evolution into two different directions.   The actual course of
evolution, consequently, takes place in-between these two trends, as
sketched in Fig.13, p.43 and Fig.16.
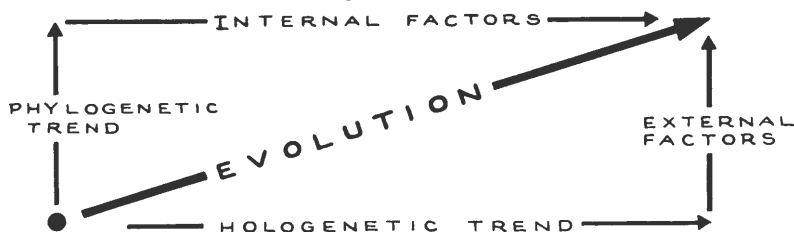


Figure 16.   Presumed interaction of internal and external factors on the
course of evolution (according to Leppik, 1957b).

From several taxonomic orders proposed by de Candolle (1827),
Prantl (1888), Hallier (1905), Hutchinson (1926), and others for classi-
fication of the family Ranunculaceae, the newly revised grouping of
Janchen (1949) appears most appropriate for the study of floral evolution.
In this system, for instance, the genus Paeonia is joined with the Ranun-
culaceae, against the suggestion of Wordsell (1908) to segregate this
genus as a separate unigeneric family Paeoniaceae.

In the following taxonomic conspectus of the Ranunculaceae special
attention is called to floral structures and typological characteristics.
Main type-classes of flowers are used in their historical sequence:
amorphic→haplomorphic→actinomorphic→pleomorphic→stereomorphic→
zygomorphic, as pictured in Fig.1, p.7.   Subfamilies are indicated with
capital letters, tribes with consecutive Arabic numerals, subtribes with
small letters.   The number of species in every genus is included in
parenthesis that follows generic names.


### Family Ranunculaceae


Flowers hypogynous, haplomorphic, actinomorphic, pleomorphic,
stereomorphic, or zygomorphic.   Sporophylls and semaphylls in lower
levels numerous and indefinite, becoming differentiated and specialized
in higher levels.   Fruit an achene, follicle, or berry.   Mostly herba-
ceous, occasionally woody plants (Paeonia) of wide distribution, but most
abundant in the forested parts of the north temperate zone.

A. HYDRASTIDOIDEAE.   Outer integument longer than the inner.
   Perianth (Perigon) simple, tri- or tetramerous.   No bracts, no
   nectar-leaves.   Carpels free or grown together.   Fruits one- or
   many-seeded berries.

1. Hydrastidae. Flowers pleomorphic, sepals 3, petal-like, petals none, stamens and pistils numerous.

   a. Glaucidiinae. Fruit achene, many-seeded. Glaucidium (1). Distributed in Asia.
   b. Hydrastidinae. Fruits 1-2-seeded berries. Hydrastis (2). Perennial herbs with a solitary terminal flower. One species occurs in North America, another in eastern Asia.

B. PAEONIOIDEAE. Outer integument longer than the inner. Flowers haplomorphic, actinomorphic, or pleomorphic. No nectar-leaves, but well developed "ringnectaries." Carpels several, fruits many-seeded.

   2. Paeonieae. Single genus Paeonia (33) in Eurasia, tree peonies in China.

C. ANEMONOIDEAE. Flowers in lower levels actinomorphic or pleomorphic, in higher levels seldom stereomorphic (Myosurus). Outer integument shorter than the inner. Perigon mostly corolla-like. Nectar-leaves none, or present. Fruits achenes or berries.

   3. Clematideae. Perigon mostly corolla-like, pleomorphic. Nectar-leaves none or very small.

      a. Thalictrinae. Perigon 4-5, small, pleomorphic but unshowy. Nectar-leaves none. Anemonella (1), Piuttia (1), Thalictrum (120).
      b. Anemoninae. Perigon 5-6, mostly actinomorphic or pleomorphic. Nectar-leaves small or absent. Anemone (100), Hepatica (6), Pulsatilla (7), Miyakea (1), Barneoudia (5), Capethia (2), Knowltonia (13).
      c. Clematidinae. Perigon 4 or more, pleomorphic. Nectar-leaves small. Clematopsis (16), Clematis (400).
      d. Kingdoniinae. Perigon 5 or 2, pleomorphic, nectar-leaves none. Kingdonia (1), Circaeaster (1).

   4. Ranunculeae. Perigon mostly sepal-like, seldom corolla-like. Flowers actinomorphic or pleomorphic, stereomorphic in Myosurus, showy. Nectar-leaves present, showy, petal-like, seldom absent.

      a. Ranunculinae. Flowers mostly pleomorphic, showy. Nectar-leaves with grove, petal-like, showy. Trautvetteria (2), Kumlienia (1), Arcteranthis (1), Cyrtorrhyncha (1), Halerpestes (6), Oxygraphis (9), Paroxygraphis (1), Aphanostemma (1), Batrachium (5), Ranunculus (300), Ficaria (10), Beckwithia (2), Gampsoceras (1), Ceratocephalus (2), Casalea (3), Myosurus (17), Hamadryas (6), Krapfia (1).
      b. Laccopetalinae. Flowers large, Magnolia-like, haplomorphic or actinomorphic. Nectar-leaves with numerous groves. Laccopetalum (1).

  c. Adonidinae. Flowers actinomorphic or pleomorphic. Nectar-
     leaves with one grove on each, corolla-like. Callianthemum (16),
     Adonis (40).

D. HELLEBOROIDEAE. Flowers haplomorphic, actinomorphic, pleo-
   morphic or zygomorphic. Nectar-leaves mostly present, showy,
   corolla-like. Carpels 3-5, seldom 1-2, fruits, follicles or berries.

  5. Isopyreae. Flowers pleomorphic or stereomorphic (Aquilegia).
     Nectar-leaves cup-like or absent.

     a. Cimcifuginae. Nectar-leaves very short, cup-like.
        Xanthorrhiza (1), Coptis (15), Beesia (2), Souliea (1),
        Cimcifuga (20), Actaea (11), Anemonopsis (1).
     b. Helleborinae. Nectar-leaves tubulate. Helleborus (26),
        Eranthis (2), Shibateranthis (1).
     c. Isopyrinae. Flowers pleomorphic or steromorphic (Aquilegia).
        Nectar-leaves cup-like, sometimes with spur. Enemion (7),
        Asteropyrum (2), Isopyrum (26), Leptopyrum (1), Paropyrum (1),
        Paraquilegia (4), Semiaquilegia (3), Urophysa (2), Aquilegia (120).

  6. Trollieae. Flowers actinomorphic, pleomorphic or secondarily
     haplomorphic (Trollius). Nectar-leaves flat.

     a. Calthinae. Flowers actinomorphic or pleomorphic. Nectar-
        leaves flat or absent. Caltha (40), Calathodes (3), Trollius (29),
        Hegemone (1).
     b. Nigellinae. Flowers pleomorphic, nectar-leaves 2-lobed.
        Komaroffia (2), Nigella (22), Garidella (2).
     c. Delphiniinae. Flowers stereomorphic or zygomorphic.
        Nectar-leaves with spur or coiled. Aconitum (350), Delphinium
        (380), Consolida (60).

                              DISCUSSION

     A mere glance at the above described holetic groupings of ranalian
flowers (Fig.13) and a comparison of this system with other flowering
plants, reveal an obvious central position of the Ranunculaceae in this
assemblage. In a general way, ranalian plexus has produced a sequence
of flower types that represents the basic trend in the floral evolution of
angiosperms. This is actually an amplification of one of the main con-
clusions drawn by Braun (1858), restated by Arber and Parkin (1907-
1909) in their strobiloid theory, and ascertained by Zimmermann (1935-
1961) after an extensive phylogenetic study. But it has been only very
recently that the basic trend of floral evolution could be correlated with
the concurrent sensory development of pollinating insects, as described
elsewhere (Leppik, 1957b).
     The gradual evolution of various floral structures in close correlation
with the sensory development and abilities of pollinating insects is so
convincingly demonstrated in the Ranunculaceae that the "old great mys-
tery of flowers" as still emphasized by modern writers (see Just, 1939,

1952; Good, 1956; Pijl, 1960, p.414), seems reliably explained now. All types of structural modifications and special devices of insect-pollination, such as showy semaphylls, nectar-leaves, concealed nectaries, nectar guides, and other complicated pollination mechanisms are represented in ranalian flowers in all phases and stages of development. There is good evidence to assume that all these complicated contrivances, adjusted to their particular pollinators, have evolved in response to the selective activity of their permanent visitors. The whole evolutionary sequence of ranalian flowers does not reveal any point that would support the antiselectionistic theories of Goebel (1915-1920), Troll (1928), Werth (1956), and others, reviewed and criticied by Pijl (1960, p.403ff.).

On the other hand, it is fairly evident that anthophilous insects, birds, bats, and other flower visitors must distinguish and remember a number of floral characteristics to locate their food plants from a multitude of flower types exposed to them in a foraging area. Special senses for form, symmetry, color, taste, odor, and numerical patterns have developed in these insects step by step during their long sensory evolution that has lasted several hundred million years. Finally, a well-perfected sensory mechanism has evolved in anthophilous insects that governs their food-searching (trophoclectic) instincts and regulates their selective activity among flowers.

Thus, a well-perfected system of flower types has evolved in the ranalian plexus in close correlation with the sensory development of pollinating insects, as pictured in Fig. 11. This system corresponds to the gradual sensory development of anthophilous insects in their successively acquired ability grades to distinguish amorphic, haplomorphic, actinomorphic, stereomorphic, and zygomorphic flower types. Once fixed in insects as inherited instincts and senses, these perceptive faculties guide pollinators in their food-searching and selective activity. Numerous observable progressive and regressive trends, sometimes even the recapitulation of the whole evolutionary sequence, testify to such selective activity of various groups of pollinators in the present-day floras.

Gradual development of inherited instincts and special senses has enabled anthophilous insects to correlate their selective activity through countless generations in the same principal line, as expressed in the historical sequence of floral evolution. In the lower evolutionary levels, the trophoclectic instincts and elementary senses for color, odor, taste, form, size, and symmetry must have been much the same in all insect groups that possess compound eyes and other sense organs of similar structure. This can be concluded from the similar sensory reaction of all recent primitive insect groups to elementary flower types on haplomorphic and actinomorphic levels.

But the sensory reaction of pollinators to the floral characteristics became more and more specific on and above the pleomorphic evolutionary level, reaching its maximum diversity in the zygomorphic type-class. The zoophilous flower classification according to their visitors, was first introduced by Delpino (1868-1874), and adapted more recently by Vogel (1954), Kugler (1955), and Pijl (1960); therefore it is reasonably justified only for flowers on the upper evolutionary levels. But it is unfit for the classification of flowers on lower levels that are accessible to

all pollinators. This shortcoming of Delpino's system is also indicated by Werth (1956), who introduced an artificial morphological system for floral classification. But this system, in its turn, is inapplicable for evolutionary study. The obvious advantage of the classification of flower types according to their historical development and evolutionary sequence, as proposed in the present study, appears from the comparison of all systems mentioned.

Such comprehensive knowledge about the floral evolution enables us now to resolve some controversial viewpoints and conflicting theories about flowers. The typological concept of Goethe (1790), "concetto biologico" of Delpino (1868-1870), the "Gestalttypus" of Troll (1928), and "Stil" of Vogel (1954), although criticized by Pijl (1966ff) for their anti-selectionistic attitude, still have some basic virtue. By the limitations of their time, these authors could not know, and not even suspect, the existence of such efficient sensory systems in insects, as established later by sensational discoveries of von Frisch (1954), Lindauer (1955), Lindauer and Kerr (1960), and others.

The great merit of the typological conception of Goethe and the Gestaltehre of Troll lies in the emphasis on a certain regulating principle or law in nature that governs the evolution of flower types. "If this key principle could be found, the interpretation of the flower might enter upon a new and more hopeful phase" (Arber, 1936, p. 182). Now the key principle is found in the regulating sensory perception mechanisms of pollinators and reinterpretation of the flower is in full swing.

Some practical aspects of these new findings, particularly a new discipline, "bee-botany," are reviewed and discussed recently by Deodikar (1961). This author purposely correlates recent discoveries in the sensory physiology of insects with the newest achievements in floral ecology thus elaborating a new bottom-ground for the further progression of apiculture.

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Regardless of all these valuable comments and corrections the writer accepts the whole and sole responsibility for the contents of this paper and the ideas expressed. In debatable areas, therefore, the writer relies on his own experience and observations, in a sense, as formulated in several previous reports.

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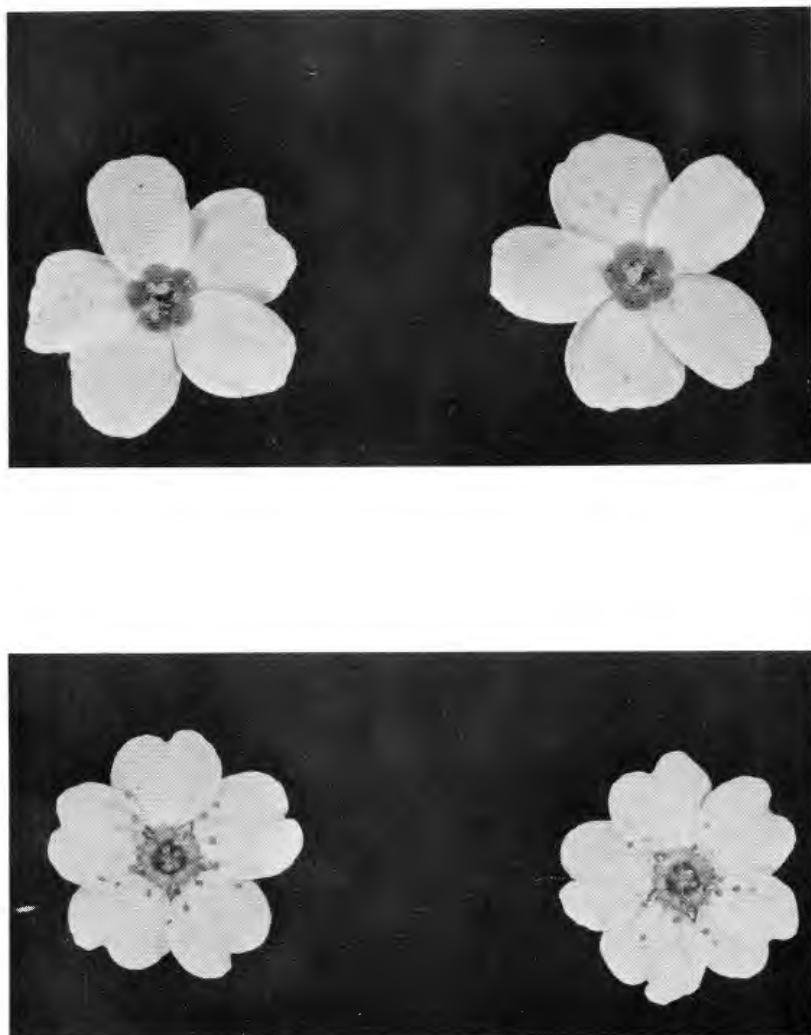
Plate 1.  Inflorescences of _Euphorbia_ _corollata_ L. (above 3x enlarged)
imitating pentamerous flowers of _Spirea_ _trilobata_ L. (below, 3x
enlarged).  Both structures resemble in form (pentamerous), color
(white, with yellow center), and size (about 1 cm in diameter).  All
plates are reproduced from photographs processed in Iowa State
University Photolab.

Plate 2.  Magnolia soulangeana Soulg. (above) compared with the inflor-
      escence (flower head) of Tithonia speciosa Hook (Compositae, be-
      low).  Note the similar haplomorphic form and symmetry in both
      structures.  Both photographs are of natural size.
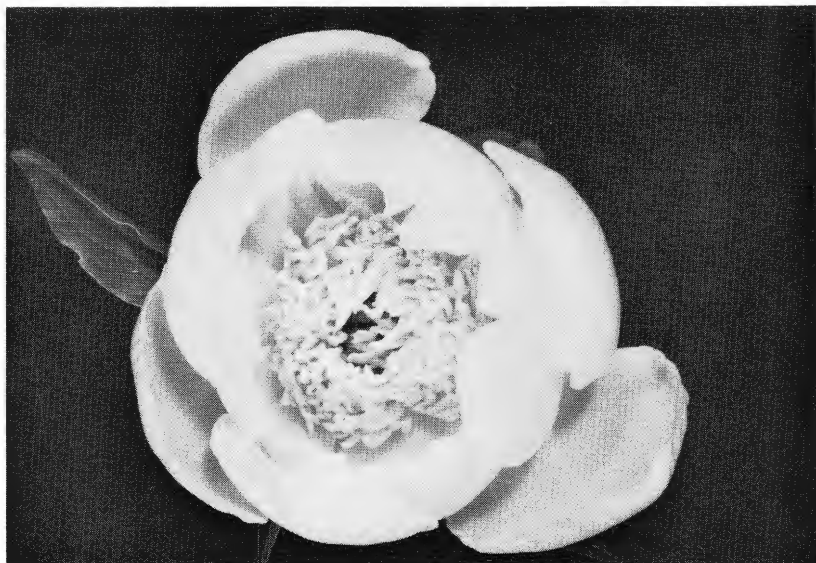
Plate 3.  Above <u>Paeonia</u> <u>potanini</u> Komarov, var. <u>alba</u> F.G. Stern in hap-
        lomorphic stage.  Below <u>P</u>. <u>albiflora</u> Pall. in actinomorphic stage.
        Both stages, although belonging to the same genus and resembling
        in size and color, differ in form and are thus distinctive to hymen-
        opterous pollinators.  Both photographs slightly reduced.

Plate 4. A flower of <u>Trollius</u> <u>chinensis</u> Ledeb. (above) compared with the flower head of <u>Calendula</u> <u>officinalis</u> L. (below). Both structures look much alike, although belonging to different families, and are composed of different morphological organs (flower vs. inflorescences.) Both photographs are slightly reduced.
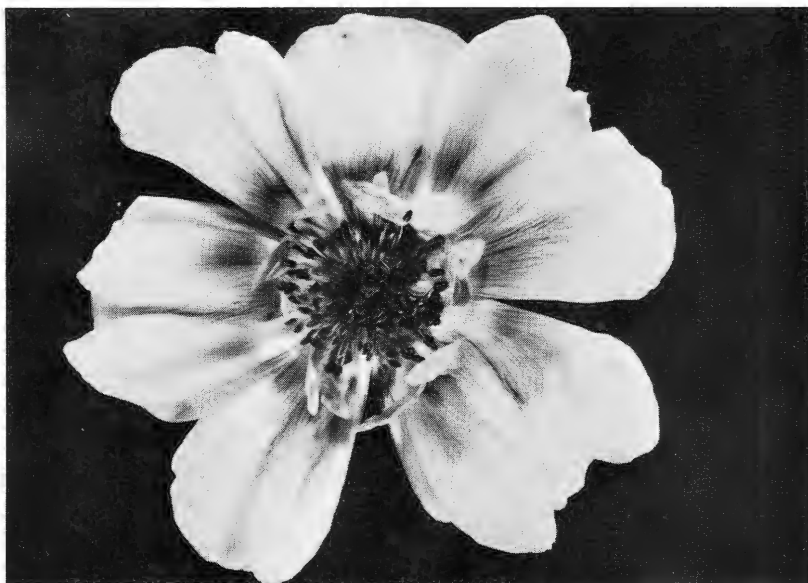
Plate 5.  Anemone blanda Sch. and Ky. (above) single flower is com-
pared with flower head of Gaillardia sp. (below); both are actino-
morphic.  Both photographs about natural size.
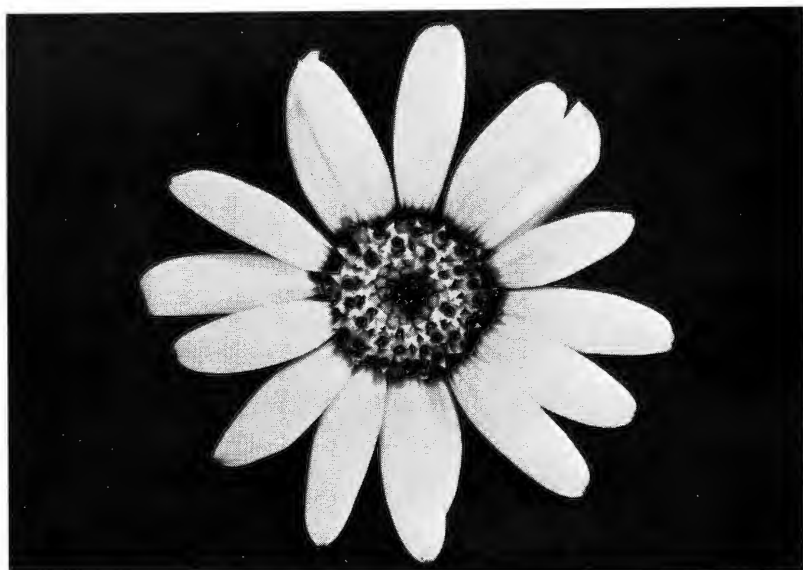
Plate 6. *Anemone* *apennina* L. (above) single flower compared with flower head of *Dimorphotheca* *aurantiaca* DC. (below); both actino-morphic. Both photographs 2x enlarged.
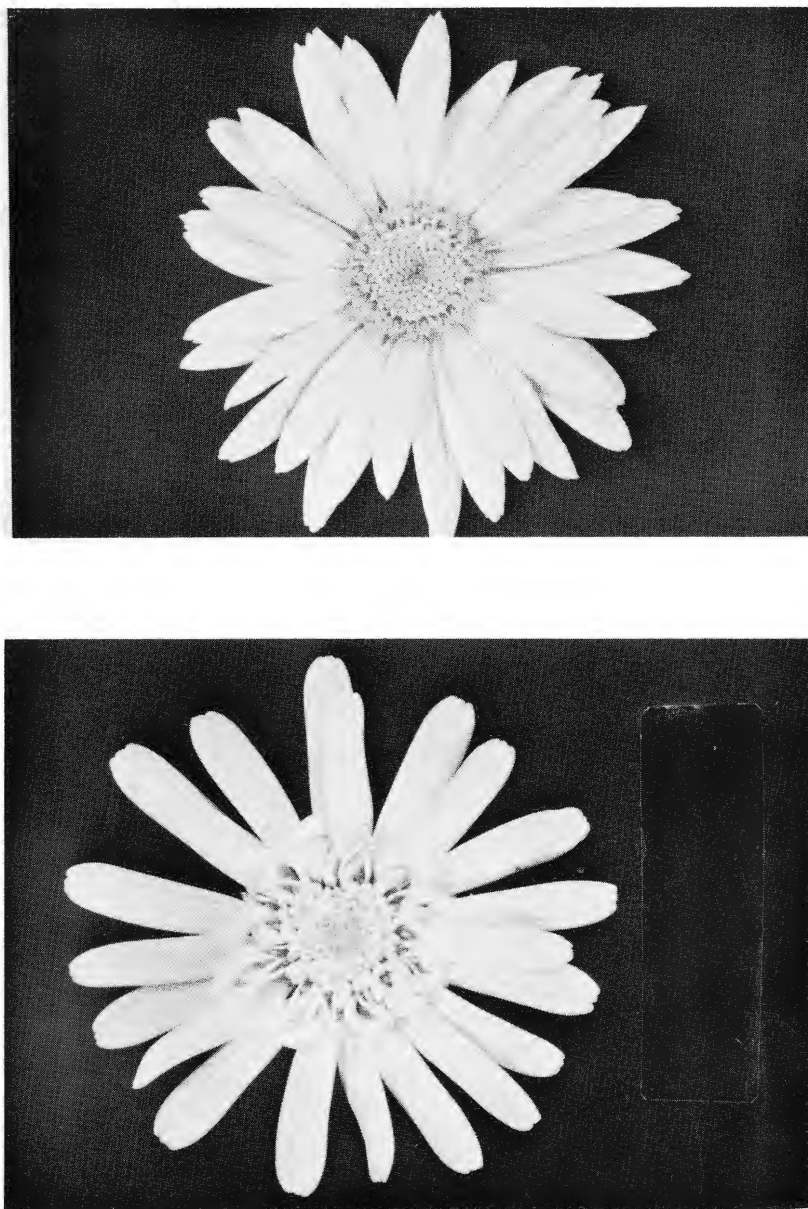
Plate 7.  Pyrethrum roseum Lindl. (above) is compared with Chrysan-
themum thunbergi Lindl. (below) both actinomorphic.  Both photo-
graphs 2x enlarged.
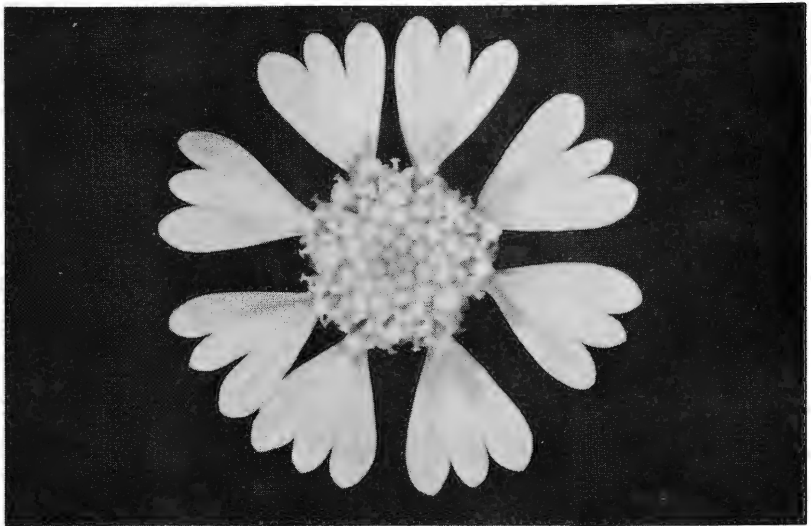
Plate 8. Helenium autumnale L. (above) is compared with Actinea odorata L. (below). Both flower heads are of pleomorphic form, with delicately emarginated rays, but differ in the number of rays (oligomerous vs. octomerous). Both photographs 3x enlarged.

Plate 9. Octomerous single flower of Anemone japonica S. and Z. (above) is compared with octomerous flower head of Cosmos bipinnatus Cav. (below). Both pleomorphic types have striking similarity in form and symmetry. Both photographs about natural size.

Plate 10.  Anemone canadensis L.  A tetramerous (above) flower is compared with a pentamerous (below) blossom (2x enlarged).
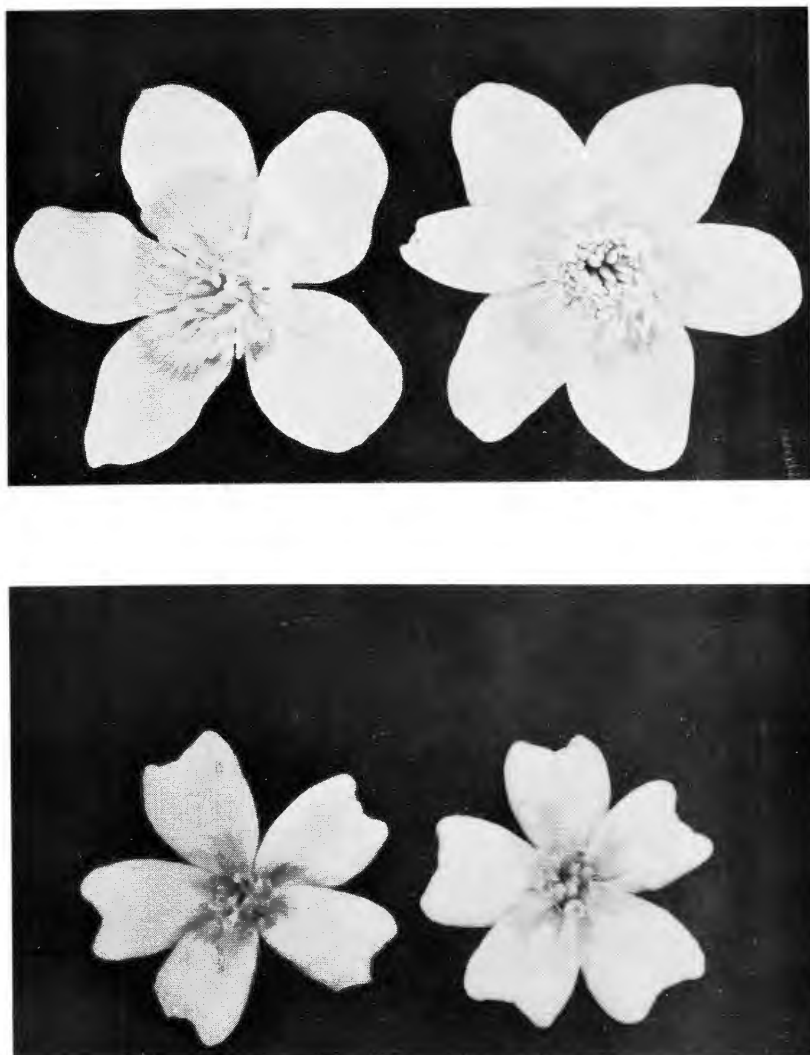
Plate 11. Euanthial flowers of _Caltha palustris_ L. (above, 2x enlarged) are compared with pseudanthial flower heads of _Tagetes signatus_ Bartl. (below, 2x enlarged). Note the striking similarity of both pleomorphic structures that have evolved in phylogenetically unrelated plant orders. Yet the shape of the somewhat wavy and undulate petals of _Caltha_ are more robust and primitive than the delicately emarginated rays of _Tagetes_.
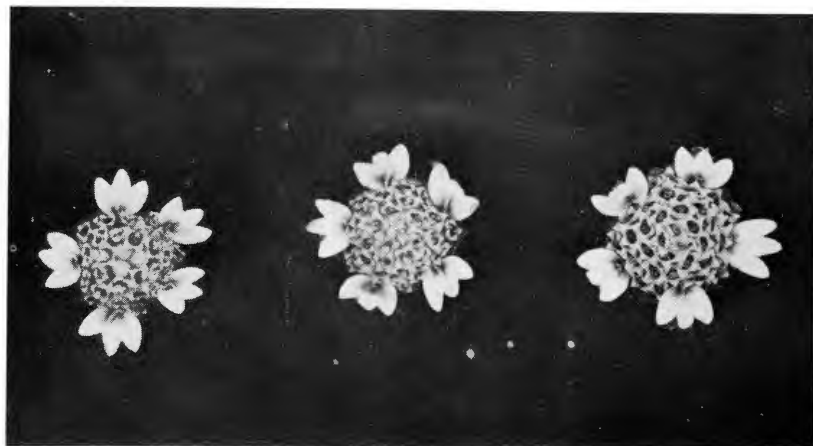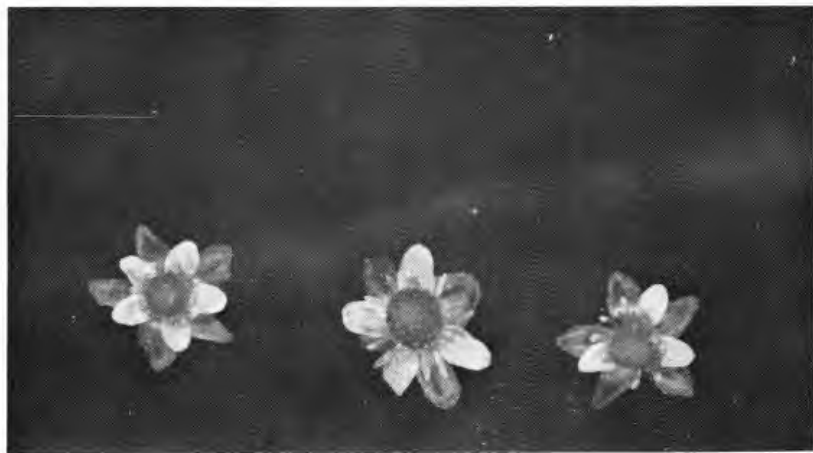
Plate 12. Micranthous pleomorphic flowers of Ranunculus sceleratus L. (above, 4x enlarged) are compared with flower heads of Galinsoga ciliata (Raf.) Blake (below, 4x enlarged). Both floral patterns are prevalently pentamerous of the same size and color, but differ in the shape of semaphylls. The petals of the Ranunculus are simple, ovate with entire margin, while the more perfected rays of Galinsoga are delicately trilobate. This characterizes the different evolutionary stage of the Ranunculaceae and the Compositae in their historical stage of development.
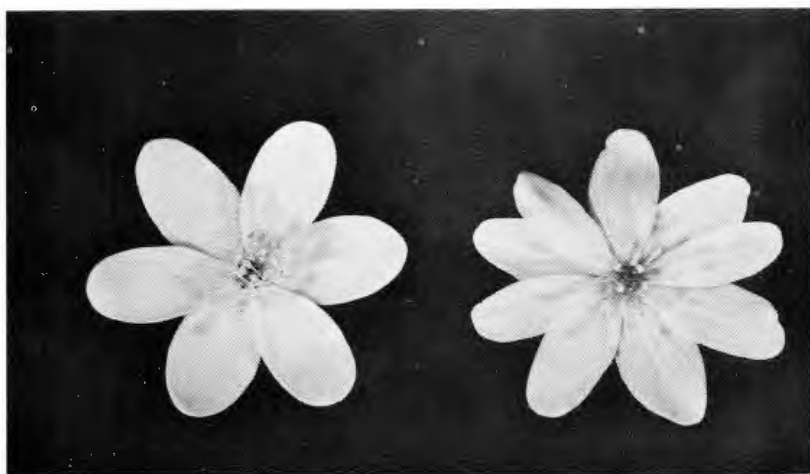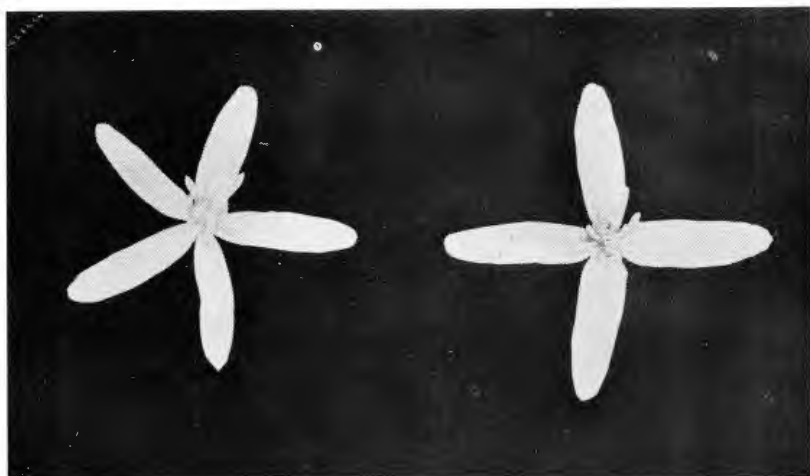
Plate 13. Pleomorphic flowers of Clematis recta L. (above, 2x enlarged). Flowers prevalently pentamerous (left), infrequently tetramerous (right). Hepatica triloba Chaix. (below, 2x enlarged). Number of petals varies from 6-11.
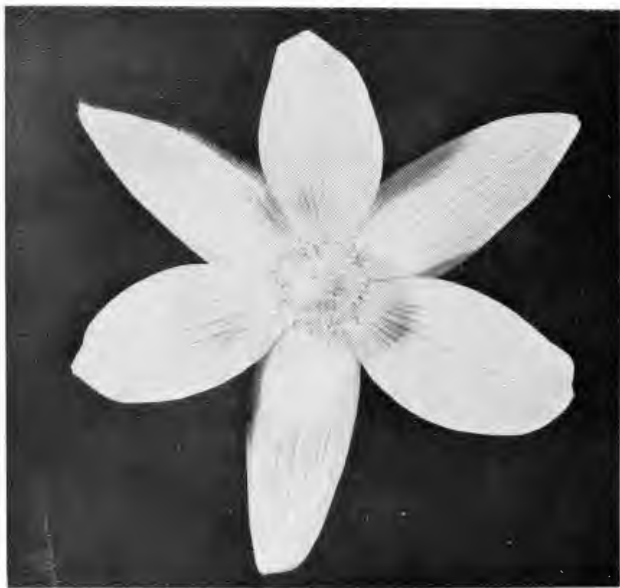
Plate 14. Anemone (Pulsatilla) patens L.  Floral shape (above) and profile (below), slightly enlarged.
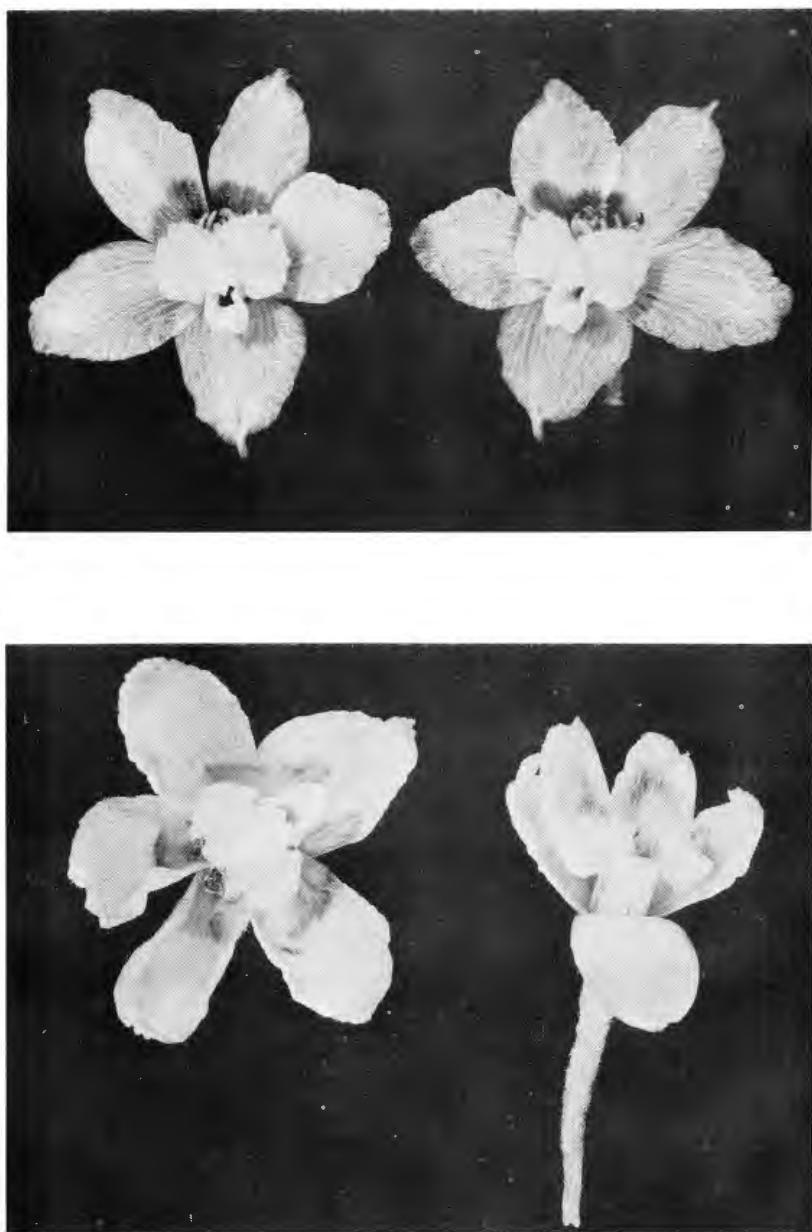
Plate 15. Bilateral flowers of _Delphinium_ sp. with an elongated spur (below, right), slightly enlarged.

Plate 16.  Delphinium sp. cult.  A white garden variety with polymorphic flowers.  Above:  front view of a flower.  Below:  a honeybee as a rare visitor of the "man made" flower (see in text p. 25).
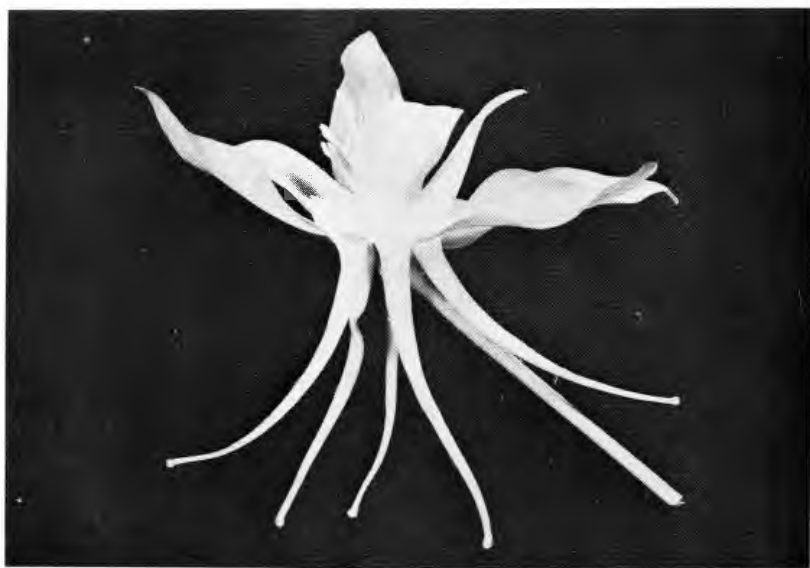
Plate 17. Stereomorphic flower of Aquilegia hybrida Sims, from above and in profile, slightly enlarged.

Plate 18.  Aconitum napellus L.  Above links: a flower from side view.
Antirrhinum majus L.  Above right: a flower from front view.
Below: the same flower photographed from side view (see in text
p. 35).

Plate 19. Antirrhinum majus L.   Above links a flower with closed
     "parlor," right an opened flower.   Below a bumblebee entering
     into the "floral parlor" (see explanation in text p. 35).

Plate 20. Above: marking of a honeybee with white spot on thorax.
Below: a marked bee is preparing to fly away. (See explanation
in text pp. 9-13.)

Plate 21. Selected scenes from the "struggle of bees." Above: a general turmoil in a bee colony photographed on the flying board of a bee hive. In the middle; several fighting scenes with attacking and stinging bees (1, 2, 3, 4), redrawn from a photograph. Below: a photograph showing an attacking bee stinging a victim. Photographs taken in Weihenstephan, Germany (see explanation in text p. 11).
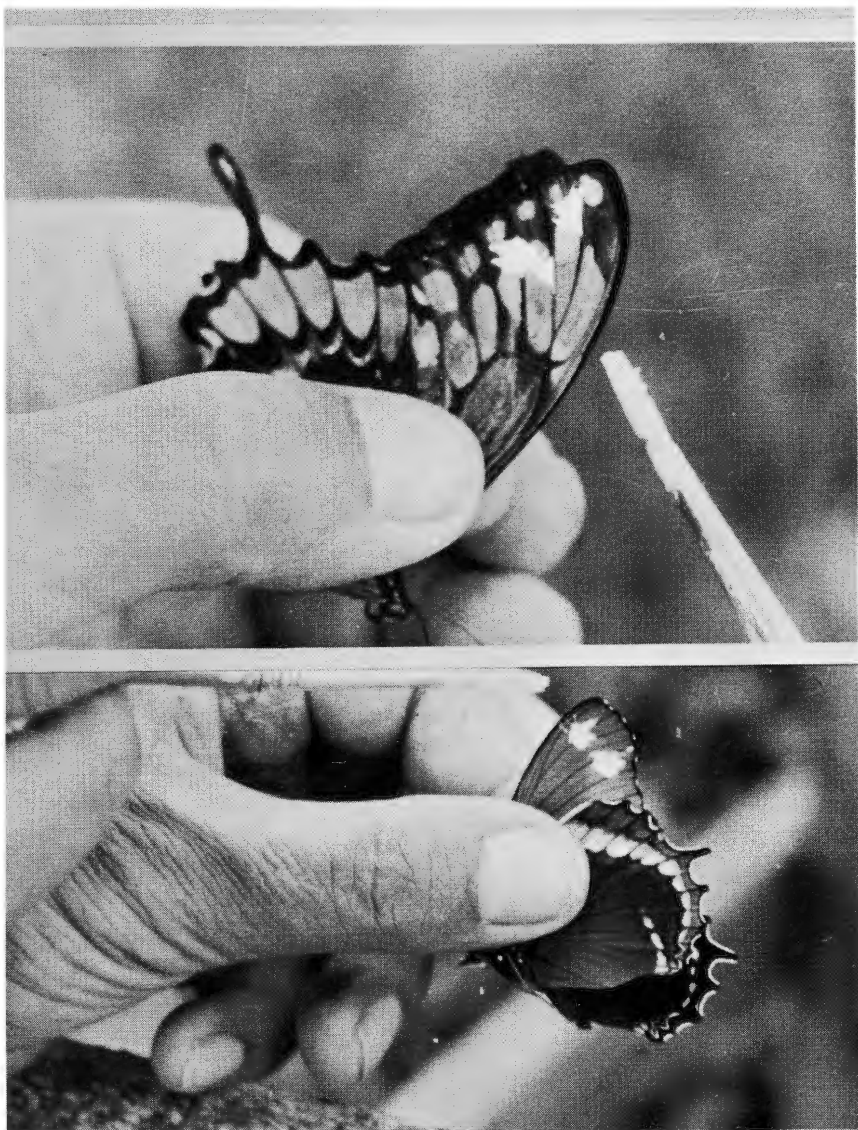
Plate 22. Marking of butterflies for observation at the Tropical Research
        Institute of the University of San Salvador in Central America.
        Above; Papilio thoas autocles R. & J. Below: Victorina ephas
        Lattr. (see explanation in text p. 50).
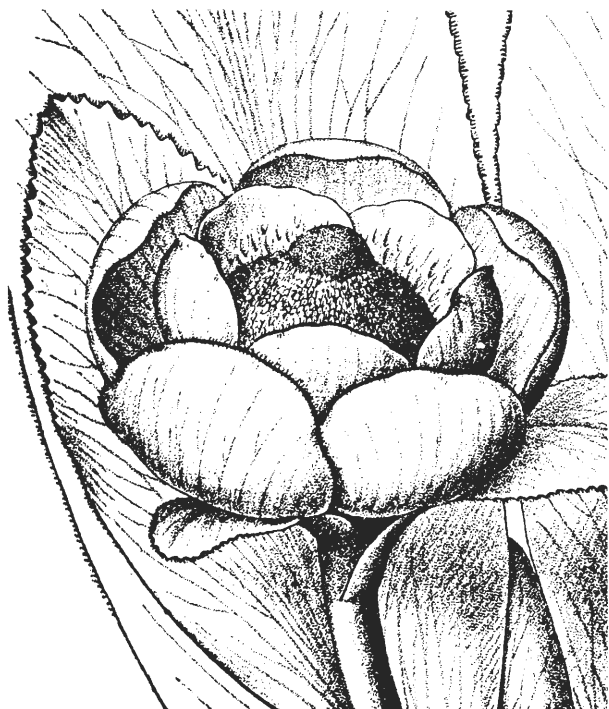
Plate 23.  Laccopetalum giganteum Ulbrich (1906). A giant haplomorphic greenish-white flower, up to 5 inches in diameter, resembling the Magnolia blossom, rather than buttercup flowers.  Some flowers are reported as reaching 7 inches and more in diameter if fully expanded.  This coarse shrub with large spatulate leaves (2 feet or more in length) occurs in the high mountains of Peru, South America.  Reproduced from the picture by Ulbrich (1906, pp.405-406) (see text pp. 44 and 59).
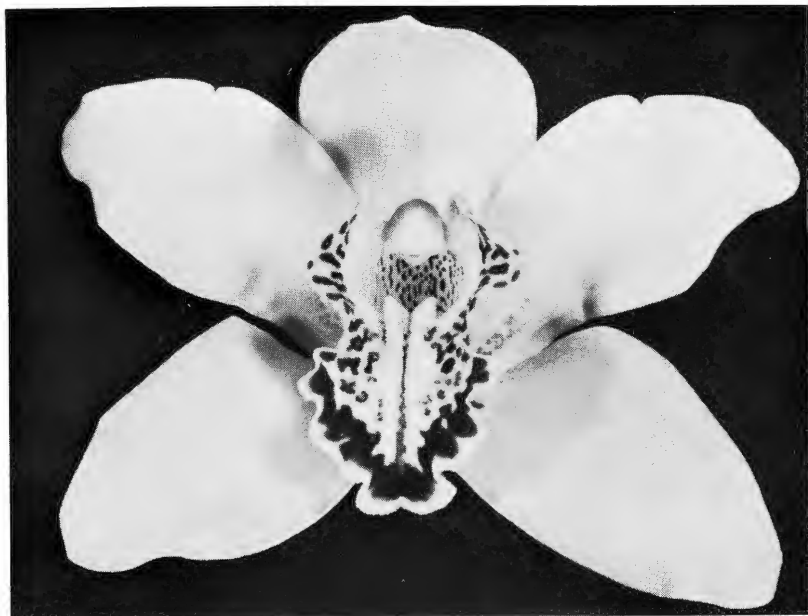
Plate 24. Transformation of pleomorphic ranalian flower patterns into a simple zygomorphic type in the Orchidaceae. One petal (in the middle) is transformed into an ornamented zygomorphic corolla. Above is pictured a flower of Cymbidium sp. cult. 'Bodmin Moor' of the Dos Pueblos Orchid Company, Goleta, California. Below is Epidendrum radicans Ldl. with zygomorphic petal (lower lip) on pentamerous pattern (see text p. 36).

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